SHOUT
SHARE
IT

S.BM.1015

BRITISH MUSEUM
GENERAL
28 SEP 1981
LIBRARY
NATURAL HISTORY

Bulletin of the British Museum (Natural History)

Entomology series Vol 42 1981

British Museum (Natural History)
London 1981

Dates of publication of the parts

No 1	29 January 1981
No 2	26 February 1981
No 3	30 April 1981
No 4	25 June 1981

ISSN 0524-6431

Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

CENTRAL
1981
LIBRARY

Contents

Entomology Volume 42

Page

No 1 A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations.
Michael C. Day 1

No 2 A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region.
Barry Bolton 43

No 3 A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae).
J. Mark Ritchie 83

No 4 A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae).
Angoon Lewvanich 185

BRITI
GENER
2 9 JAN
LIBRAR
NATUR

Bulletin of the British Museum (Natural History)

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations

Michael C. Day

Entomology series
Vol 42 No 1

29 January 1981

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Ent.)

© Trustees of the British Museum (Natural History), 1981

ISSN 0524-6431

Entomology series
Vol 42 No 1 pp 1–42

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 29 January 1981

BRITISH M
GENERA
2 9 JAN
LIBRARY
NATURAL HIS

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations

Michael C. Day

Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis 1
Introduction 1
The nomenclatural history of the family name 2
  Psammochares and Psammocharidae versus *Pompilus* and Pompilidae . . 2
  The type-species of the type-genera 4
The family-group names of the Pompilidae 5
Genus *Pompilus* Fabricius 7
  Key to species of *Pompilus* 10
    Females 10
    Males 10
Nomenclatural changes in genera other than *Pompilus* 36
Acknowledgements 37
References 37
Index 41

Synopsis

The genus *Pompilus* Fabricius is redefined to include seven Old World species, of which six are known in both sexes; males of four are described or associated for the first time and a seventh species is described as new from a single female. Keys and distributional data are given. Biology is summarized; that of the type-species is treated at length, including development of the mature larva. One new generic and sixteen new specific synonyms are established and lectotypes are designated for five nominal species; one new combination is made. The nomenclatural histories of alternative family names and of their type-species are summarized and a catalogue of family-group names is given. The possible affinities of *Pompilus* are discussed. For other genera an improperly proposed generic name is made available, a further generic and specific synonymy are established, and three new combinations made; two lectotypes are designated.

Introduction

The spider-hunting robber wasps constitute a family of aculeate Hymenoptera of considerable morphological homogeneity. The family names Pompilidae and Psammocharidae have both at various times been applied to the group in which their type-genera, *Pompilus* Fabricius, 1798 and *Psammochares* Latreille, 1796, have each been used as 'blanket' genera for very large numbers of species. Following issue of Opinion 166 (1945) of the International Commission on Zoological Nomenclature (ICZN), usage has largely stabilized in favour of *Pompilus* and Pompilidae. In order to clarify modern usage for future students, I have thought it worthwhile to give an historical account of nomenclatural applications of *Pompilus* and *Psammochares* and their derivative family names. A catalogue of other extant family-group names is appended for completeness.

In recent years, *Pompilus* has progressively been more rigorously defined such that fewer and fewer species have been assigned to the genus. However, workers have failed to consider the

Bull. Br. Mus. nat. Hist. (Ent.) **42** (1): 1–42

Issued 29 January 1981

generic placement of some species thus excluded which are extralimital to their particular regional interest. Such excluded genera and species are all considered here. *Pompilus* is redefined in its most restricted sense, and a preliminary assessment given of the genera to which it is most probably related. No complete account exists of the type-species or its congeners, which are here described and keyed and their distribution summarized. A full account is given of the biology of the type-species since previous reports conflict in certain respects.

I have again in general followed the terminology of Evans (1966); morphological terms are herein abbreviated as follows.

SGP subgenital plate
SMC submarginal cell

Depositories in which material studied is housed have been abbreviated as follows:

AM	Albany Museum, Grahamstown
ANS	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
BPBM	Bernice P. Bishop Museum, Honolulu
CAS	California Academy of Sciences, San Francisco
MCZ	Museum of Comparative Zoology, Harvard
MHN	Muséum d'Histoire Naturelle, Geneva
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin
MRAC	Musée Royal de l'Afrique Centrale, Tervuren
NMB	Naturhistorisches Museum, Basle
NMR	National Museum of Rhodesia, Bulawayo
NMW	Naturhistorisches Museum, Vienna
NR	Naturhistoriska Riksmuseum, Stockholm
RNH	Rijksmuseum van Natuurlijke Historie, Leiden
RSM	Royal Scottish Museum, Edinburgh
SAM	South African Museum, Cape Town
TMP	Transvaal Museum, Pretoria
TMU	Tokyo Metropolitan University, Tokyo
UM	University Museum, Oxford
USNM	United States National Museum (of Natural History) Washington
UZM	Universitetets Zoologisk Museum, Copenhagen
ZI	Zoological Institute, Leningrad
Colln Empey	Collection of H. N. Empey, Johannesburg
Colln Wahis	Collection of R. Wahis, Chaudfontaine

The nomenclatural history of the family name

The first spider wasps described were placed by Linnaeus (1758) in his genus *Sphex*. Latreille (1796), in proposing *Psammochares* and *Ceropales*, recognized two fundamental groupings of these wasps and differentiated them from *Sphex* s.l. He diagnosed the groups but included no species. Fabricius (1798) proposed *Pompilus* for a group of 37 species, mostly spider-hunting wasps, which he stated was 'Genus Sphegibus nimus affine'. The subsequent nomenclatural history of *Psammochares* and *Pompilus* is confused, hingeing on two problems; firstly, the seniority and availability of the names, and secondly, the type-species designations for the genera and their identities. I hope the following is both a definitive and a fair account which will explain the present application of the name *Pompilus* and clarify aspects of the nomenclatural history not presently well documented.

Psammochares and Psammocharidae versus *Pompilus* and Pompilidae

Latreille (1802–3: 334) diagnosed *Pompilus* and wrote 'Exemple, *Pompilus viaticus* F. Remarq. J'avais établi le premier ce genre sous le nom de *psammochare*. J'abandonne volontiers cette dénomination pour prendre celle de *pompile*, qui est plus douce à l'oreille'. Subsequently (1803*b*:

158) he gave a similar account, but in more detail. Part of this account has been quoted by Pate (1946), but he failed to quote the last four sentences, as follows. 'M. Fabricius en sépara ces insectes disparates; mais il n'épura pas encore parfaitement le genre, puisqu'il y laissa des insectes qui ont bien des très-grands rapports avec les *sphex,* mais dont les parties de la bouche sont très-différents, *sphex sabulosa, sphex fusca.* J'entrepris de terminer la réforme et je créai le genre *psammochare* (qui aime le sable), en prenant pour type le dernier insecte que je viens de citer [Pate's quotation concludes]. Kirby, en Angleterre, s'est occupé peu de temps après, et sans connaitre mon travail, du même sujet. Il a donné le nom *d'ammophile* aux *sphex* de M. Fabricius qui ont leurs machoires et leur lèvre inférieurs allongées, fléchies. L'entomologiste de Kiell a fait de mes *psammochares* des *pompiles,* et son genre *sphex* à cette séparation près, est resté le même. Je viens de le restreindre . . . '.

It is clear that Latreille's primary objective was the definition of two distinct but similar groups of fossorial Hymenoptera. However he anticipated the possible confusion that might result from the proposal by Kirby (1798) of a name for one of the groups which meant the same as that proposed by Latreille himself for the other, i.e. *Ammophila* and *Psammochares,* 'sand lover'. In rejecting both these names, and employing the names used by Fabricius, Latreille was of course not in accord with current nomenclatural procedure. However, as a pioneer of many aspects of taxonomic practice, the act was laudable as one of selfless rejection of his own proposal in order to reduce confusion to a minimum. This seems not previously to have been understood as such; previous authors have noted only Latreille's remarks concerning the euphony of *Pompilus* compared with *Psammochares.*

Most early authors followed Latreille unquestioningly; few chose even to cite *Psammochares* as a synonym of *Pompilus.* Throughout the nineteenth century hundreds of species names were proposed in *Pompilus,* which was also employed as the stem of the family name Pompilidae, despite the fashion for employing the oldest included genus, in this case *Ceropales* Latreille, 1796. In 1901, Fox stated his belief that *Pompilus* was preoccupied in the Cephalopoda by a supposed genus *Pompilus* Schneider, 1784. In the first decade of this century *Aporus* Spinola, 1808 and *Ceropales* Latreille were each on occasion employed for the traditional blanket genus *Pompilus,* and Aporidae and Ceropalidae were both employed as family names. However, in 1910 Banks resurrected *Psammochares* and based a family name Psammocharidae on it. In the two subsequent decades, substantial progress was made in the taxonomy of spider wasps, with virtually all important contributions employing *Psammochares* and Psammocharidae. However, the identity of the type-species had not properly been elucidated. No author (save Banks in his last works) employed the generic name for the group to which it should properly have been applied other than as a blanket genus-name approximating to the present tribe Pompilini. Nevertheless, it was the earliest available name, valid under the law of priority.

In 1935, the ICZN considered a general petition concerning hymenopterous names, initiated in 1928 by J. C. Bradley and bearing 59 other signatures, requesting various actions under suspension of the rules, including the suppression of *Psammochares,* the validation of *Pompilus,* and designation of a type-species for the latter. No specific reason was given for the proposed action; one is left to infer that the substitution of *Psammochares* for *Pompilus* had been a bad thing! This unfortunate petition was to result in the issue of several opinions of which no. 166 (1945) adopted the course submitted for *Pompilus.* The history of this case and its needless consequences are a lesson in the pitfalls that attend those who would suspend the rules of nomenclature. Townes (1957*a*; 1969) has expounded at length credible reasons for regarding as invalid the opinions resulting from the 1935 Lisbon International Congress of Zoology, at which Bradley's petitions were first considered. The submission was insufficiently advertised in advance of the Lisbon congress, at which the ICZN decided in principle to suspend the rules. During the congress material changes were made to the original submission (substitution of *P. pulcher* F. for *S. viatica* L. as type-species, for reasons explained below). Finally, following subsequent sufficient advertisement, objections were received from the committee on nomenclature of the Entomological Society of Washington and from C. D. Michener. The latter stated succinctly '*Psammochares* is the name now in general use and is correct without a suspension of the rules'. Nonetheless, it was judged that no new material evidence had been presented and in 1945 the Lisbon decision was given effect over the signature of the secretary, F. Hemming, without further reference to the Commissioners. He appended a scholarly refutal of the existence of the spurious homonym, *Pompilus* Schneider, which was shown to be a trivial name combined with *Octopodia* Schneider, and thus also of no relevance to the case.[1] Despite the inutility of the decision and the unsatisfactory nature of its promulgation, most subsequent works save those of Banks (1946), Pate (1946) and Townes (1957*a*; 1957*b*; 1973) have followed Opinion 166.

Resubmission of the case to the ICZN would not be without precedent. The names *Sphex* and *Ammophila* were subject of an Opinion, no. 32 (1910), which ruled on the identities of their type-species, but without suspension of the rules. Subsequently, this Opinion was superseded by Opinion 180 (1946) which suspended the rules in order to alter the applications previously decreed. However, it is likely that any reconsideration of the controversial Lisbon decisions by the ICZN would take account of usage subsequent to the issue of the Opinion(s) in question, which thus offers little hope of a remedy. Where a dichotomy of interpretation exists, a final solution must necessarily be arbitrary; I therefore follow the existing majority practice, with the proviso that the lessons of this nomenclatural tangle be learned. These are, simply that reference to the ICZN should be a last resort, required only when application of the *Code* gives no solution to intractable problems. In particular, thorough scholarship is essential in determining all aspects of the case in order to anticipate further ramifications. Many submissions relate to nomenclatural inconveniences that are of a purely temporary nature in terms of potential future usage. Only those who view the future of mankind with extreme pessimism have real grounds for consideration of current expediency as a basis for future stability – and such pessimists have little future need of zoological nomenclature in any event.

The type-species of the type-genera

The previous paragraphs relate the sequence of applications of generic and suprageneric names without reference to the precise identities of those entities. The following considerations are rendered redundant by Opinion 166, but for the sake of historical clarity are given in detail.

As previously stated, Latreille (1796) included no species in *Psammochares,* whilst Fabricius (1798) included 37 in *Pompilus.* Latreille later (1802–03: 334–335) equated his *Psammochares* with *Pompilus* and by implication included in it the 37 species of Fabricius. He cited *S. viatica* 'F' as an 'Exemple'. On p. 332 of the same work, under '*Sphex* alongés' he cited *S. arenaria* F. as an 'Exemple' of one part of this group of sphecids; this species was later differentiated by him (1809) from *S. viatica* 'F.', but shown to be the same as '*S. viatica* L.' of authors such as DeGeer. Most authors have rejected Latreille's 'Exemple' as valid type-species designation, save in Latreille (1810) (ICZN Opinion 11, 1910). Latreille (1803*b*: 158) wrote the passage quoted earlier at length, in which 'en prenant pour type le dernier insecte' (*Sphex fusca* L.) he again chose a species clearly to be interpreted as a spider-wasp. He had earlier (1803*a*: 354–355) confused several entities but with no contained type-species designation. Later (1805: 280) he cited nine species in *Pompilus,* all undoubted spider-wasps. Fabricius (1804: 187 *et seq.*) placed 63 species of diverse affinities, but predominantly spider-wasps, in *Pompilus.* His twelfth species, *viaticus,* had the mouth parts described in detail. Malaise (1937) has given reasons for regarding this as a type-species designation for *Pompilus;* however, this view is not current. Finally, Latreille (1809: 55) clarified the situation with regard to *S. viatica* L. and *S. viatica* 'F.' Thus, of the possible acceptable type-species designations for *Pompilus,* none is of a species which is not now interpreted as a spider-wasp, or as a deliberate misidentification of one (*S. viatica* 'F.'). Thus, under current rules, there is no nomenclatural mechanism to prevent application of the name to a group of spider-wasps. I incline to the view that Latreille (1803*b*) designated *S. fusca* L. type-species of *Psammochares,* in which he had earlier included Fabricius's 37 species by reason of his effective replacement of *Psammochares* by *Pompilus;* he may thus be judged simultaneously to have designated a type-species for *Pompilus*. Nevertheless, Pate (1946) argued that *Pompilus* should be applied as a genus in the Sphecidae, since he believed *S. viatica* L. to be designated type-species, and he interpreted this to be the species currently known as *Podalonia hirsuta* (Scopoli). It is certainly because of this controversy that, at the last minute, the type-species cited in Bradley's petition to the ICZN on *Pompilus* (*S. viatica* L.) was changed to *P. pulcher* F. This latter was probably selected because Šustera (1912) had in error cited *S. plumbea* F. as type-species of *Psammochares*! *S. plumbea* was not an originally included species in *Pompilus,* but *P. pulcher,* a synonym, was. Subsequent authors of important works, such as Haupt (1927), had followed this usage. It is unfortunate that no type-specimen exists for this taxon, the ultimate basis of the family name.

---

[1] *Octopodia pompilus* (L.) Schneider [*Nautilus pompilius* L., 1758]; other Schneider names of 1784 are suppressed by ICZN Opinion 233, 1954.

Townes (1973) reiterated and developed Pate's views. I have elsewhere (1979*a*; 1979*b*) given an account of the history of *Sphex viatica* and *Sphex fusca.* I do not doubt that, in the absence of Opinion 166, both *Psammochares* and *Pompilus* (type-species *Sphex fusca* L. [= *Anoplius viaticus* (L.) of current usage]) would be senior names for the genus currently known as *Anoplius* Dufour and within this group for the subgenus *Arachnophroctonus* Howard (= *Pompilinus* Ashmead). The ICZN (1980) has since issued Opinion 1157, ruling on the validity of conflicting lectotype designations for *Sphex viatica* L.

The family-group names of the Pompilidae

Much of the work produced on this family has dealt with local faunas, and the classifications employed have thus tended to be superficial assessments. Certain recognizable kinds of morphology (which often prove to be parallel developments in different zoogeographic regions) have at various times been recognized as suprageneric categories. The names employed for these categories have often been proposed without reference to previously available names or, occasionally, have been re-proposed independently. Often one name has been applied by different authors to groups with little or nothing in common. The classification of the Pompilidae is not yet at a stage which permits stable employment of these names; few groups are well defined save perhaps the currently recognized subfamilies Pompilinae, Pepsinae and Ceropalinae. However, since these names are relatively few in number, they are here listed in chronological order as a guide for other workers. This should facilitate their subsequent correct employment provided the *International Code of zoological Nomenclature* is followed. Subsequent usages and independent subsequent proposals are not listed.

Pompilii Latreille, 1805: 277. Type-genus: *Pompilus* Fabricius, 1798 (Pompilidae).

Most past workers have credited Leach (1815) with authorship of this group-name, despite the fact that Latreille first applied suprageneric names in the Hymenoptera based on the stem of an included genus. In the introduction (p. vj) of volume 3 of his *Histoire naturelles* (1802–03), he wrote '. . . j'ai créé d'autres coupes générales, et plusieurs nouveaux genres; j'ai surtout donné le premier, en cette partie, l'idée d'une division par familles'. On p. x, 'La dénomination des familles que j'ai cru devoir former est composée du nom du genre dominant, et d'une finale. Il faut soulager la mémoire et ne pas surcharger sans nécessité la nomenclature'. In 1805, he employed Pompilii as a latinization of *Pompilus* and gave 'Pompiliens' as a vernacular name. He included the genera *Thynnus* F., *Pompilus* F. and *Ceropales* Latreille. I have no hesitation in recognizing Latreille, 1805 as author of the family name Pompilidae (Article 36, *Int. Code zool. Nom.*).

Aphorida (sic) Leach, 1815: 149. Type-genus *Aporus* Spinola, 1808. (Aporini).

An incorrect original spelling of Aporida Leach.

Pepsites Lepeletier, 1845: 464. Type-genus: *Pepsis* Fabricius, 1804 (Pepsinae).

Ceropalidae Radoszkowski, 1888: 489. Type-genus: *Ceropales* Latreille, 1796.

Notocyphini Fox, 1894: 296. Type-genus: *Notocyphus* Smith, 1855.

[Ageniinae Ashmead, 1900: 154. Type-genus: *Agenia* Schiødte, 1837.]

Unavailable; based on a junior homonym of *Agenia* Dezcourtilz, 1825.

Planicepinae Ashmead, 1900: 155. Type-genus: *Planiceps* Latreille, 1825 [= *Aporus* Spinola, 1808].

Anopliini Ashmead, 1902: 80. Type-genus: *Anoplius* Dufour, 1834.

Homonotini Ashmead, 1902: 131. Type-genus: *Homonotus* Dahlbom, 1843.

Chirodamini Ashmead, 1902: 135. Type-genus: *Chirodamus* Haliday, 1837.

[Psammocharidae Banks, 1910: 114. Type-genus: *Psammochares* Latreille, 1796.]

Suppressed by ICZN Opinion 166, 1945.

Ageniellini Banks, 1912: 222. Type-genus: *Ageniella* Banks, 1912.

Deuteragenini Šustera, 1912: 176. Type-genus: *Deuteragenia* Šustera, 1912 [=*Dipogon* Fox, 1897].

Macromerinae Haupt, 1927: 23. Type-genus: *Macromeris* Lepeletier, 1831.

[Claveliinae Haupt, 1929: 111. Type-genus: *Clavelia* Lucas, 1851.]

Permanently rejected under Article 40, *Int. Code zool. Nom.* through supposed synonymy of type-genus; see Ctenocerinae Arnold, 1934*b* [1929].

[Pedinaspinae Haupt, 1929: 112. Type-genus: *Pedinaspis* Kohl, 1884 [= *Entomobora* Gistel, 1857].]

Permanently rejected under Article 40, *Int. Code zool. Nom.* through synonymy of type-genus; see Entomoborini Pate, 1947 [1929].

[Platyderini Haupt, 1929: 112. Type-genus: *Platyderes* Guérin-Méneville, 1844 [= *Ferreola* Lepeletier, 1845].]

Unavailable: based on a junior homonym of *Platyderes* Stephens, 1827; see Ferreolini Priesner, 1969.

Epipompilini Haupt, 1930: 724. Type-genus: *Epipompilus* Kohl, 1884.

Psilotelini Arnold, 1932: 44. Type-genus: *Psilotelus* Arnold, 1932.

Ctenocerinae Arnold, 1934*b* [1929]: 386. Type-genus: *Ctenocerus* Dahlbom, 1845.

Replacement name for Claveliinae Haupt, 1929, q.v.

Cryptocheilinae Banks, 1934: 4. Type-genus: *Cryptocheilus* Panzer, 1806.

Hemipepsini Banks, 1934: 5. Type-genus: *Hemipepsis* Dahlbom, 1843.

[Pseudageninae Banks, 1934: 31. Type-genus: *Pseudagenia* Kohl, 1884.]

Permanently rejected under Article 40, *Int. Code zool. Nom.* through synonymy of type-genus: see Auplopodini Pate, 1946.

Priocnemini Banks, 1934: 31. Type-genus: *Priocnemis* Schiødte, 1837.

Eidopompilini Arnold, 1936*a*: 73 (as Idopompilini) Type-genus: *Eidopompilus* Kohl, 1899.

Haupt (1930) made the emendation *Idopompilus* of Kohl's genus *Eidopompilus;* Arnold based his tribal name on Haupt's unjustified emendation.

[Calicurgini Haupt, 1937: 66, 69. Type-genus: *Calicurgus* Lepeletier, 1845.]

Unavailable; based on a junior homonym of *Calicurgus* Brullé, 1833.

Cordyloscelini Arnold, 1937: 75. Type-genus: *Cordyloscelis* Arnold, 1935.

Teinotrachelini Arnold, 1937: 75. Type-genus: *Teinotrachelus* Arnold, 1935.

Psammoderini Arnold, 1937: 76. Type-genus: *Psammoderes* Haupt, 1929.

Pseudopompilini Arnold, 1937: 76. Type-genus: *Pseudopompilus* Costa, 1887.

Tachypompilini Arnold, 1937: 76. Type-genus: *Tachypompilus* Ashmead, 1902.

Spuridiophorini Arnold, 1937: 77. Type-genus: *Spuridiophorus* Arnold, 1934.

Apinaspini Banks, 1938: 238. Type-genus: *Apinaspis* Banks, 1938.

[Ctenoceratini Bradley, 1944*a*: 30. Unjustified emendation of Ctenocerinae Arnold, 1934*b* [1929] q.v.]

Allocharini Bradley, 1944*a*: 29, 147. Type-genus: *Allochares* Banks, 1917.

Allocyphonychini Bradley, 1944*a*: 29, 150. Type-genus: *Allocyphonyx* Ashmead, 1902 [= *Paracyphononyx* Gribodo, 1884].

Anoplageniini Bradley, 1946: 125. Type-genus: *Anoplagenia* Bradley, 1946 [= *Priochilus* Banks, 1944].

Auplopodini Pate, 1946 [1934]: 117. Type-genus: *Auplopus* Spinola, 1841.

Replacement name for Pseudageninae Banks, 1934, q.v.; however, Pate referred to a subsequent erroneous usage of Pseudageniini (Bradley, 1944*b*). Bradley had confused *Pseudagenia* and *Deuteragenia*! Pate did not note the confusion.

Pilpomini Pate, 1946: 117. Type-genus: *Pilpomus* Costa, 1859 [= *Auplopus* Spinola, 1841].

Alternative, conditionally proposed, to Auplopodini Pate, q.v.

Pedinaspidinae Pate, 1947: 18. Emendation of Pedinaspinae Haupt, 1929.

Entomoborini Pate, 1947 [1929]: 18. Type-genus: *Entomobora* Gistel, 1857.

Replacement name for Pedinaspinae Haupt, 1929, q.v.

[Paraferreolini Haupt, 1949: 65, 73. Type-genus: *Paraferreola* Šustera, 1912.]

Paraferreola Šustera is based on a misidentified type-species and should be applied in the Mutillidae; it is not currently applied in the Pompilidae (Pate, 1946). The name *Tea* Pate, 1946 is currently used for the species previously placed in *Paraferreola,* as a subgenus of *Eoferreola* Arnold. This genus, together with *Arachnotheutes* Haupt and *Stolidia* Priesner, is allied to *Pseudopompilus* Costa, for which a tribal name was proposed by Arnold, 1937, q.v.

Batozonina Haupt, 1950: 49. Type-genus: *Batozonus* Ashmead, 1902 [= *Poecilopompilus* Howard, 1901].

Batozonus is currently placed as a synonym of *Poecilopompilus* Howard (Evans, 1966); the name Episyronina Haupt, 1950, q.v., based on a related currently valid genus, is to be preferred should a supra-generic name be required for the group of genera of which these are part.

Episyronina Haupt, 1950: 56. Type-genus: *Episyron* Schiødte, 1837.

Minageniini Townes, 1957*a*: 221, 225. Type-genus: *Minagenia* Banks, 1934.

Auplopini/Auplopiini Haupt, 1959: 17. Incorrect subsequent spellings of Auplopodini Pate, 1946 [1934] q.v.
Ferreolini Priesner, 1969 [1929]: 120. Type-genus: *Ferreola* Lepeletier, 1845.
Replacement name for Platyderini Haupt, 1929, q.v.
Psoropempulini Evans, 1975: 263. Type-genus: *Psoropempula* Evans, 1975.

Genus ***POMPILUS*** Fabricius

Pompilus Fabricius, 1798: 212. Type-species: *Pompilus pulcher* Fabricius, 1798 [= *Sphex cinerea* Fabricius, 1775: 350], by subsequent designation (ICZN Opinion 166, 1945).
Chionopompilus Priesner, 1955: 15, 164. Type-species: *Chionopompilus rabinovitchi* Priesner, 1955 [= *Pompilus niveus* Saunders, 1901], by original designation. **Syn. n.**

♀♂. Length 3–24 mm. Ground colour black, with more or less white/grey/grey-blue pubescence, otherwise black/dark brown pubescent. Wings hyaline, slightly fusco-hyaline or flavo-hyaline with infuscate tips. Tibial spurs brown with grey pubescence, stramineous, or white; appendages occasionally with a pinkish ground colour. Female head with eyes sub-parallel or converging above, in males sometimes wider above than below. Malar space sometimes developed, clypeus transverse, truncate or emarginate, labrum entire with weak median emargination, more or less exposed, sometimes reflexed downwards from clypeal margin. Mandible arcuate, elongate, thin, yellow or light brown, darker apically, with a single internal tooth remote from well-developed pointed tip. Female antennae normal, male often thicker distally. Pronotal hind margin angulate. Postnotum transverse, less than length of metanotum, often narrowest in midline. Propodeum convexly rounded, sometimes with a little flattening of the declivity, often with a dorsal median sulcus; declivity never markedly concave or with lateral backward directed teeth. Wings with three SMCs, third narrower than second. Female foretarsus with well-developed tarsal comb-spines, male often with some similar development. Female terminal tarsal segments with a single central longitudinal row of many very fine spines beneath, much smaller and more numerous than those of preceding segment, sometimes lost posteriorly; male lacks spines beneath. Female claws dentate or toothless. Male terminal foretarsal segment normally symmetrical, but fore claws symmetric or asymmetric (inner strongly cleft, outer semi-bifid); other claws dentate or semi-bifid. Female sixth tergum with dorsal surface most frequently covered in hairs modified as globular or leaf-like black or brown adpressed backwardly directed scales, often totally obscuring surface beneath; occasionally only little more developed than conventional pubescence. Male SGP (Fig. 31) with pair of antero-lateral, posteriorly directed lobes or hair-tufts; surface centrally elevated, opaque; laterally flat, transparent: with some posteriorly directed hairs centrally, and some short stout spinous hairs terminally. Genitalia, see Fig. 30.

Pompilus is here restricted to a group of seven species, and is readily recognized as a member of the Pompilini by the criteria of all recent authors. Within the tribe females may be told by the combination of a unidentate mandible, rounded propodeum, general distribution of cinereous pubescence, sixth tergum with modified pubescence, and fifth tarsal segments with minute spines beneath. The cinereous pubescence and rounded propodeum with transverse postnotum will serve to identify males. Because of their small size and agility, males are collected relatively less frequently than the females in relation to their abundance in nature.

DISTRIBUTION. Widespread in sandy habitats throughout the Old World, with a concentration of species in Africa.

BIOLOGY. Species so far recorded are fossorial, stocking short burrows in sand with single spiders of various families.

AFFINITIES. It is clear from the nomenclatural history that *Pompilus* has been used as a blanket genus containing widely different forms. Fixation of a type-species by the ICZN had in part as its objective the assurance of continued usage of the name for a large and important genus of Pompilidae. However, the type-species selected has in fact few closely related species. As early as 1942, Wilcke restricted its use to a single species in Holland, placing all the other Dutch species once considered part of *Psammochares* by Haupt (1927) in other genera. Evans (1951) considered six other groups of species as subgenera, together with a nominate subgenus equivalent to *Pompilus* sensu Wilcke; subsequently, he added a seventh subgenus (1953*a*). Four of these, *Xenopompilus* Evans, *Perrissopompilus* Evans, *Xerochares* Evans and *Hesperopompilus* Evans, are comparatively rare Nearctic forms, largely characteristic of arid regions and of rather uncertain affinities. The remaining three, *Arachnospila* Kincaid, *Anoplochares* Banks and *Ammosphex* Wilcke are predominantly temperate Holarctic groups although *Arachnospila*-like forms are found in the Neotropics and *Ammosphex* penetrates to the Kenyan Highlands. *Pompilus* s. str. is widely distributed throughout the Old World, both temperate and tropical. Evans was followed for some time, until Priesner (1968) began to use *Arachnospila* as a genus containing the European subgenera recognized by Evans, save *Pompilus* s.str. which was used as previously by Wilcke. The species of *Arachnospila, Anoplochares* and *Ammosphex* form a fairly discrete natural assemblage, with some other Palaearctic forms such as *Pamirospila* Wolf and *Melanospila* Wolf. In particular, they have a black ground colour with black or red anterior abdominal terga, whereas *Pompilus* is normally of black ground colour with more or less grey or grey-blue pubescence. The pubescence of *Arachnospila*-group species is normally dark brown, black or reddish and does not contrast with the ground colour. Many other groups of Pompilidae, however, share a *Pompilus*-like general colour pattern. Although superficially a most unlikely group-character, it correlates quite well with other features of a more fundamental nature, which are considered below.

Evans (1951: 209, 276, 326) drew attention to a possible relationship between *Aporinellus* Banks and *Pompilus* (including *Hesperopompilus*). He cited in particular the common possession of peculiar and striking hair-tufts on the male sub-genital plate shared by these genera. I incline to the view that this is a meaningful similarity, not a parallelism, since further groups exist in which intermediate states of other, divergent, characters may be found. In particular, some members of the Old World genus *Dicyrtomellus* Gussakowski are annectant with species of *Aporinellus*; males of these species have the peculiar hair-tufts on the SGP. *Dicyrtomellus*, as presently defined, is quite a large genus in the Old World, with many rare, undescribed or poorly-known species. They are notably of semi-arid and desert regions, and much further collecting in difficult localities will be necessary in order to elucidate their relationships. *Aporinellus* and *Dicyrtomellus* are predominantly of *Pompilus*-like colour pattern. Arnold (1937: 14) suggested a close affinity between *Aporinellus* (as *Pompiloides*) and *Dicyrtomellus*; however, he had failed to recognize the males of relevant species, and reserved judgement on this basis. He tended to give excessive weight to differences in propodeal structure. *Aporinellus* have the propodeum laterally produced rearwards to form a pair of distinct teeth between which the propodeum slopes continuously forwards to touch the metanotum, obliterating the postnotum. *Dicyrtomellus* have the declivity of the propodeum flattened or slightly concave and the postnotum developed. However, species such as *A. sexmaculatus* Spinola, 1806 have the postnotum visible. '*Pompiloides*' *validus* Arnold, 1936*b*, and *Pompilus pruinosus* Smith, 1855, are two rare Ethiopian species in which an intermediate condition is discernible. The male of *P. pruinosus* Smith is unknown, whilst '*P.*' *validus* Arnold has the male hair-tufts plainly developed. *Bambesa* Arnold is another (monobasic) genus which can be assigned to the *Aporinellus/Dicyrtomellus* group. *Guichardia* Arnold, another monobasic genus, is a synonym of *Bambesa* (see p. 36). *Aporinellus* s.l. (including *Ferreoloides* Haupt and *Ceratopompilus* Bradley) is widespread throughout the world save Australia. *Dicyrtomellus* is found in the Old World save Indonesia and Australia. *Hesperopompilus* Evans (placed by Evans as a subgenus of *Pompilus*) consists of a few rare and quite diverse elements located in south-western United States and northern Mexico. Were the type-species, *H. orophilus* Evans, encountered in the Palaearctic region, it would be assigned without hesitation to *Dicyrtomellus* by most authors. Some of the other species, however, would not unhesitatingly be so placed. Nevertheless, *Hesperopompilus* is of great interest as a *Dicyrtomellus*-like element in a region of North America which is noted for primitive faunal components which have their nearest relatives in the Middle East region of the Old World, for example *Fedtschenkia* in the Sapygidae, *Crioscolia* in the Scoliidae.

Aporinellus might be regarded as a widespread and diverse group derived from a *Dicyrtomellus*-like ancestor. Similar forms must have given rise to the highly modified oriental group of species allied to *Pompilus ilus* Bingham, which currently has no available generic name. This group of species has lost the tarsal comb and has highly modified, reduced mandibles, probably correlated with an abandonment of the fossorial habit. It is confined to the Oriental and Indonesian forest regions. It is noteworthy that despite a marked modification of the male subgenital plate, the hair-tufts remain well developed. The SGP is of a lanceolate form paralleled in some *Aporinellus* and

Dicyrtomellus.

European authors have used a subgeneric name in *Aporinellus* for the small group of Palaearctic, Oriental and Ethiopian species allied to *Pompilus hasdrubal* Kohl. So far as I have been able to determine, the name is not yet validly proposed under the *International Code of zoological Nomenclature,* since no type-species has been designated; the late H. Priesner, initiator of the name (see p. 36), included multiple species at the time of proposal (1969:84). Thus, *Amblyellus,* type-species *P. hasdrubal* Kohl by present designation, must take present date and authorship (see p. 36). *Amblyellus* has been used more recently as a genus rather than as a subgenus of *Aporinellus.* This usage emphasizes the unique form of the propodeum, which is posteriorly rounded with a barely discernible flattening of the declivity and a specialization of the postnotum, which is strongly developed centrally but becomes obsolete laterally.

Agenioidevagetes Wolf, 1978, was described for two North African species including *Anospilus compactus* Priesner. Their affinities are uncertain. However, the females are strongly *Dicyrtomellus*-like save the possession only of a single preapical tooth on the mandible, and are in this feature and general habitus quite similar to *P. mirandus,* most generalized of the species of *Pompilus* s. str. However, the propodeum is modified much as in some species of *Dicyrtomellus.* The males are of habitus very different from *Pompilus* s. str., *Dicyrtomellus*-like saving the absence of hair-tufts on the SGP.

Ctenostegus Haupt (including *Aglochares* Banks) is a large and diverse genus of Australasian *Dicyrtomellus*-like forms. Evans (1975) has revised the species of this group, which embraces a wide range of disparate morphologies, but with several strong characters in common indicating a monophyletic lineage. In any other part of the world, several generic names would be employed to treat so disparate an assemblage. It seems that when well known, the Australian Pompilidae of many groups contain annectant forms within them which bridge gaps between diverse but related species, giving rise to particular difficulty in developing classifications at the generic level. *Ctenostegus* have lost the second cubital cross vein of the forewing, the males have the SGP with hair-tufts. They thus segregate easily from the species of *Turneromyia* Banks, 1941, another large group of Australian species, which possess three SMCs and lack the hair tufts on the male SGP. The type-species, *Anoplius ahrimanes* Turner, has tubercular protuberances developed mediolaterally on the propodeum, a tendency noted in many but not all of the related species. Species of the group have been treated by Evans (1972) as components of *Pompilus* s.l. However, their affinities are unclear, and I am not convinced that this group is so closely related to *Pompilus* as superficially may appear.

The typical head shape of *Pompilus* s.str. accommodates a long, gently curved mandible which bears a single subapical tooth. In *P. cinereus,* this is employed in a modified form of prey carriage. Most fossorial Pompilidae walk backwards dragging the prey across the substrate. *P. cinereus* picks up the spider in the mandibles, holding it clear of the ground, and walks or runs forwards with it. It is not yet known whether the species of *Pompilus* other than *P. cinereus* employ forward prey carriage, but this might logically be expected from their morphological coincidence. Indeed, the mandibular difference with the inferred behavioural difference, is one of the most telling arguments for the maintenance of a discrete small genus *Pompilus* as here treated. Most or all of the fossorial allies might be expected to drag the prey backwards as previously described. The other genera here discussed predominantly have two sub-apical teeth on a broader, more curved mandible.

It is difficult at this stage to decide on the limits of genera and thus to what extent the groups here postulated to be the nearest relatives of *Pompilus* s. str. might be considered discrete genera, or members of a single, highly diversified genus *Pompilus.* I believe it to be more practical to utilize *Pompilus* for a well-defined but restricted group of definite relationship. For the present, the resultant group of genera may be regarded approximately as equivalent to other groups of Pompilini, each centred on a well-known genus, such as *Arachnospila, Anoplius, Episyron* and *Agenioideus.* It will be convenient to refer to these as genus-groups (Article 42c, *Int. Code zool. Nom.*). Thus, I regard the *Pompilus*-like genera discussed above as members of the *Pompilus* genus-group. This has the advantage of permitting a defined classification on a tentative basis, allowing scope for subsequent modification without nomenclatural complications.

In addition to the form of the male SGP, these genera are united (save some isolated species of

South African *Dicyrtomellus*) by the generally dark ground coloration and the tendency to development of grey or blue-grey pubescence.

The residual subgenera of *Pompilus* sensu Evans are rather discrete elements. *Perissopompilus* and *Xenopompilus* might best currently be placed as genera which have affinities with the *Agenioideus* genus-group. *Xerochares* may have affinities with Neotropical Pompilini; I have recently seen material from Columbia, a significant extension to the known range, southern U.S.A. and Mexico. *Hesperopompilus,* despite its diversity, should be included in the *Pompilus* genus-group. *Arachnospila, Anoplochares* and *Ammosphex* are central to the *Arachnospila* genus-group.

Key to species of *Pompilus*

Females

1 Palaearctic (excluding North Africa), Oriental, Indonesian and Australian regions 2

– Continental Africa and Madagascar 3

2 'Pygidial area' of sixth tergum with pubescence strongly modified (compare with pubescence of fifth tergum) as short, stout scales that uniformly cover and obscure upper surface of tergum; tibial calcaria white or dark; SMC 2 and SMC 3 as in Fig. 12; 2nd cubital cross-vein oblique; face as in Fig. 2; throughout the Old World . . . . **cinereus** (F.) (p. 12)

– 'Pygidial area' of sixth tergum with pubescence not or little modified as short, stout scales; tibial calcaria dark; SMC 2 and SMC 3 as in Fig. 14; 2nd cubital cross vein perpendicular; face as in Fig. 1. Oriental, Indonesian regions . . . . **mirandus** (Saussure) (p. 26)

3 Tarsal comb of three blade-like superior comb-spines, and at least five well-developed inferior comb-spines.

Almost uniformly whitish grey pubescent, with many long, erect white hairs save on dorsum of abdomen. Wings often yellowish hyaline, sometimes hyaline. Sahara desert. **niveus** Saunders (p. 35)

– Tarsal comb of three superior comb-spines, not more than two well-developed inferior comb-spines 4

4 Wings markedly yellow with infuscate tips; extensively grey pubescent, save 4th, 5th, 6th terga wholly black. Large species (14–24 mm). Central and southern Africa . **irpex** Gerstaecker (p. 33)

– Wings rarely faintly yellow, usually hyaline or slightly fusco-hyaline with infuscate tips; when extensively grey-pubescent, 4th and 5th terga similar to terga 1 to 3, 6th black . . . 5

5 Clypeus short and broad (4.0 times broad as high), labrum clearly visible; face as in Fig. 4; scales on 'pygidial area' strongly developed, distributed also on upper lateral surface of tergum; body save 6th tergum almost entirely whitish grey-pubescent, calcaria white; intercubital vein between SMC 2, SMC 3 perpendicular; SMC 3 higher than SMC 2 (Fig. 17); terminal tarsal segments lack a clearly visible row of minute spines beneath; sometimes with a tinge of yellow in forewing. Central and southern Africa, Madagascar . . . . . **cadmius** Saussure (p. 29)

– Clypeus less broad, labrum not always visible; scales on 'pygidial area' not overlapped onto lateral surface of tergum; body grey-pubescent, normally with some dark pubescence, at least anteriorly on terga 2 and 3; calcaria white, grey-pubescent or most frequently brown; intercubital vein and SMCs otherwise; terminal tarsal segments with row of minute spines beneath; wings hyaline or fusco-hyaline 6

6 Clypeal margin transverse, labrum exserted but reflexed inwards approximately at a right angle to the clypeus (Fig. 10); face as in Figs 5, 6; SMCs as in Fig. 18. Central and southern Africa 7

– Clypeal margin convexly rounded or transverse, labrum not reflexed (Fig. 11); face as in Fig. 3; SMCs as in Fig. 13. Widely distributed in Africa and Madagascar . . **cinereus** (F.) (p. 12)

7–'Pygidial area' of tergum six with hairs thickened but not scale-like; face as in Fig. 6; extensively marked with black; fore basitarsus with a row of three superior comb-spines, a row of two inferior comb-spines, and one short spine ventrally between the rows (Fig. 9). Kalahari desert . . . . **botswana** sp. n. (p. 33)

– 'Pygidial area' of tergum six with thick, scale-like hairs; face as in Fig. 5; extensively marked with grey; fore basitarsus with three superior and two inferior comb-spines. Central and southern Africa . . . . **bilineatus** (Arnold) (p. 31)

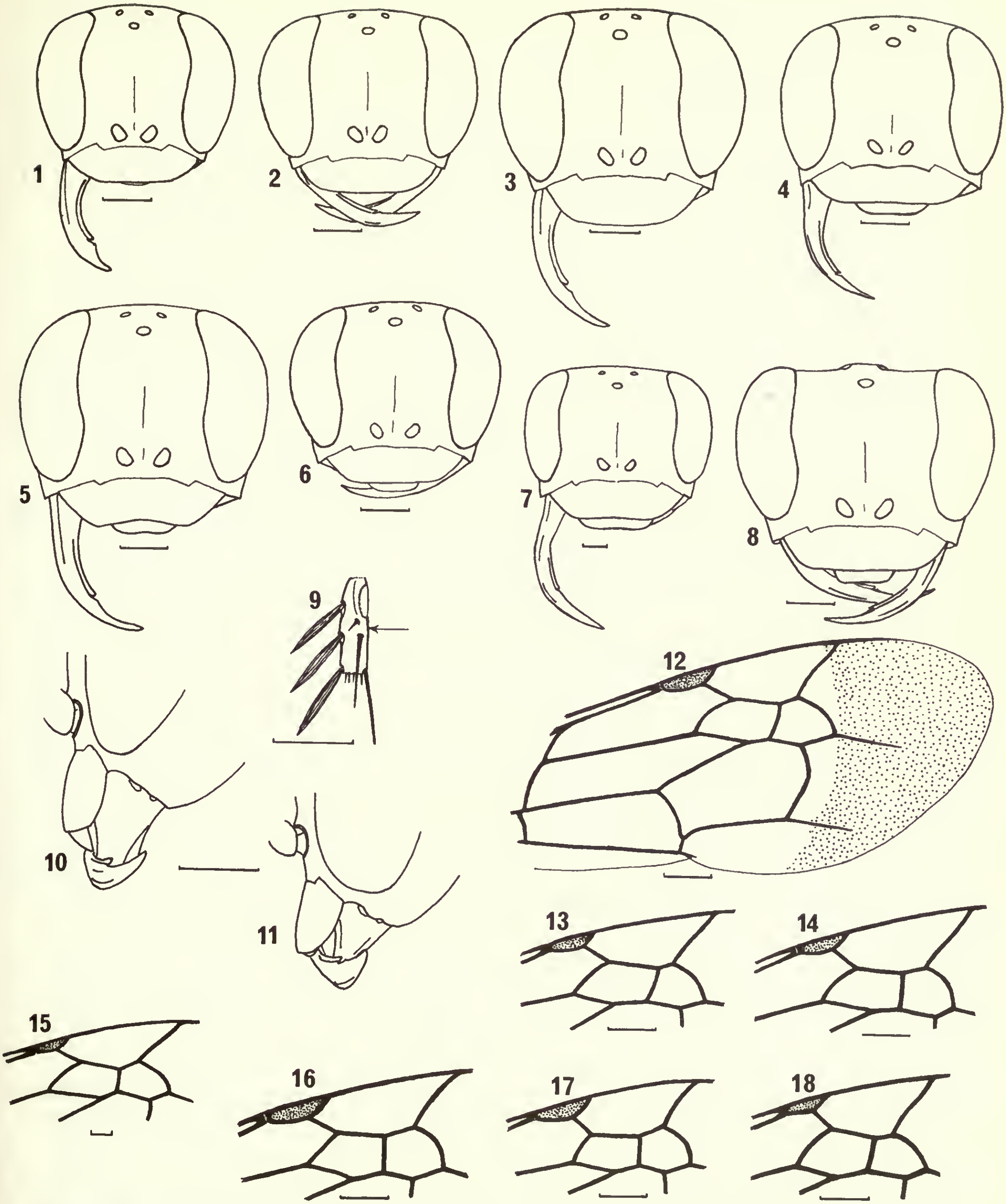
Males

The male of *P. botswana* is not yet known.

1 Palaearctic (excluding North Africa), Oriental, Indonesian and Australian regions 2

– Continental Africa and Madagascar 3

2 Face relatively broad between the eyes (Fig. 20), vertex not distinctly raised or rounded in facial view, though ocelli often demarcate a raised central platform; SMCs as in Fig. 12; terminal



Figs 1–18 *Pompilus* species, females. 1–8, head in frontal view of (1) *P. mirandus;* (2) *P. cinereus* (Oriental); (3) *P. cinereus* (Ethiopian); (4) *P. cadmius;* (5) *P. bilineatus;* (6) *P. botswana;* (7) P. *irpex;* (8) *P. niveus*. 9, left foremetatarsus, posterior view, *P. botswana*. 10, 11, labrum in lateral view of (10) *P. bilineatus;* (11) *P. cinereus*. 12, right forewing, *P. cinereus* (Oriental). 13–18, SMCs of (13) *P. cinereus* (Ethiopian); (14) *P. mirandus;* (15) *P. irpex;* (16) *P. niveus;* (17) *P. cadmius;* (18) *P. bilineatus*. Scale lines: 0.5 mm.

comb-spines of fore basitarsus clearly more than half as long as second tarsal segment. Throughout the Old World . . . . ***cinereus*** (F.) (p. 12)

– Face less broad between eyes (Fig. 19); vertex distinctly raised, rounded in facial view; SMCs as in Fig. 14; terminal comb-spines of fore basitarsus not more than half as long as second tarsal segment. Oriental, Indonesian regions . . . . ***mirandus*** (Saussure) (p. 26)

3 Fore basitarsus with comb of three strong spines, yellow distally, and with two long inferior comb-spines; body with dense, decumbent grey-white pubescence. Sahara desert . ***niveus*** Saunders (p. 35)

– Fore basitarsus usually with comb of two or three black spines, but never more than one long inferior comb-spine; body usually not entirely grey-pubescent 4

4 Clypeus short, broad, with concave margin and exserted labrum; malar space well developed (Figs 23, 24) claws of foretarsus specialized, asymmetric, of other tarsi semibifid (Fig. 26); pterostigma not or little thicker than costa plus subcosta 5

– Clypeus less broad, more or less transverse, labrum not or little exserted; malar space less well developed (Figs 21, 22); fore claws not specialized, symmetrical, others dentate or toothless (Fig. 25); pterostigma much thicker than costa plus subcosta 6

5 Wings yellow with infuscate tips; face as in Fig. 24; 1st flagellar segment 3.0 times as long as thick. Central and southern Africa . . . . ***irpex*** Gerstaecker (p. 33)

– Wings hyaline with infuscate tips; face as in Fig. 23; 1st flagellar segment less than 3.0 times as long as thick (Fig. 27). Central and southern Africa . . . . . ***bilineatus*** (Arnold) (p. 31)

6 Antennae viewed ventrally more or less strongly thickened distally (Fig. 29); SMC 2 and SMC 3 with perpendicular intercubital vein; stigma as in Fig. 17; propodeum with distinct median longitudinal groove distally; white pubescent. Central and southern Africa, Madagascar . . . . ***cadmius*** Saussure (p. 29)

– Antennae viewed ventrally not or only slightly thickened distally (Fig. 28); SMC 2 and SMC 3 with oblique intercubital vein; stigma as in Fig. 13; propodeum with a dorsal median line only; grey-pubescent. Widely distributed in Africa and Madagascar . . . . ***cinereus*** (F.) (p. 12)

Pompilus cinereus (Fabricius)
(Figs 2, 3, 11–13, 20, 21, 25, 28, 30–38)

Sphex cinerea Fabricius, 1775: 350. Holotype ♀, AUSTRALIA (BMNH) [examined].

Sphex plumbea Fabricius, 1787: 278. Holotype ♀, SPAIN (UZM) [examined]. [Synonymy by Evans, 1972: 11.]

Pompilus cinereus (Fabricius) Fabricius, 1798: 250.

Pompilus pulcher Fabricius, 1798: 249. Holotype ♀, ITALY (MNHN) [not located, presumed lost]. [Synonymy by Evans, 1972: 11.]

Pompilus pulcher Fabricius; Coquebert, 1801: pl. 12, Figs 8A, B. [Good figures, believed to be of lost primary type-specimen of *P. pulcher.*]

Pepsis plumbea (Fabricius) Fabricius, 1804: 215.

Ferreola plumbea (Fabricius) Saussure, 1867: 47; ♀.

Pompilus pruinosus Smith, 1879: 147. Holotype ♀, INDIA (BMNH) [examined]. [Junior primary homonym of *Pompilus pruinosus* Smith, 1855. Synonymy with *P. plumbeus* by Arnold, 1937: 47.] **Syn. n.**

Pompilus chevrieri Tournier, 1889: 169. Lectotype ♀, SWITZERLAND? (MHN), designated by de Beaumont, 1946: 164 [examined]. **Syn. n.**

Pompilus cinereus (Fabricius); Dalla Torre, 1897: 280.

Pompilus leprosus Dalla Torre, 1897: 298. [Replacement name for *Pompilus pruinosus* Smith, 1879.] **Syn. n.**

Pompilus plumbeicolor Dalla Torre, 1897: 311. Holotype ♀, SOUTH AFRICA (NMW) [examined]. [Proposed for *Ferreola plumbea* (Fabricius) Saussure, 1867, thought to have been a misidentification.] **Syn. n.**

Pompilus plumbeus (Fabricius); Dalla Torre, 1897: 311.

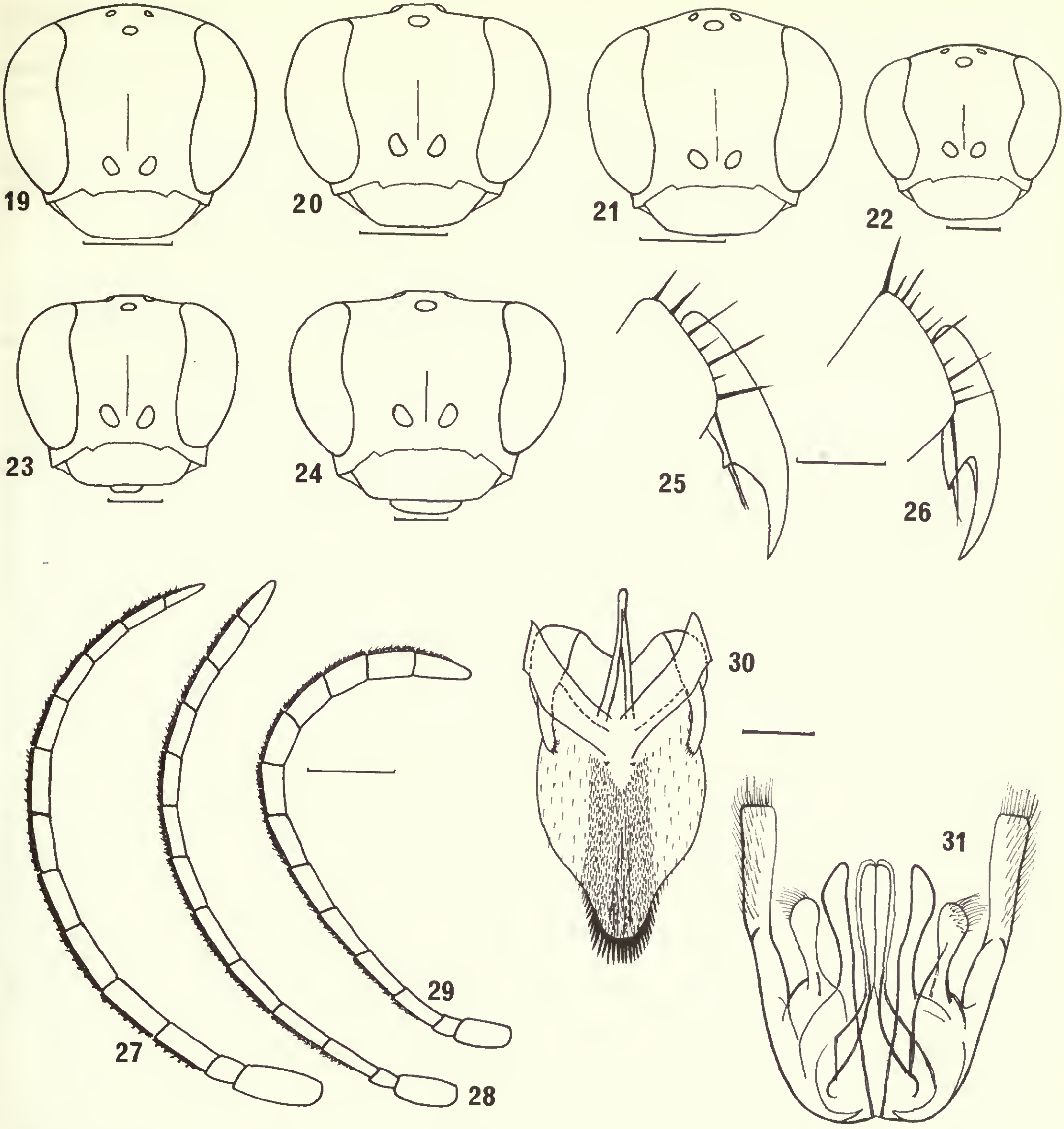
Pompilus ithonus Cameron, 1908: 301. LECTOTYPE ♀, INDIA (BMNH), here designated [examined]. **Syn. n.**

Pompilus sericeibalteatus Cameron, 1910: 250. Holotype ♂, TANZANIA (NR) [examined]. [Synonymy with *P. plumbeus* by Arnold, 1937: 47.] **Syn. n.**

Psammochares plumbeus (Fabricius) Šustera, 1912: 210. [Invalid subsequent designation of type-species for *Psammochares* Latreille, 1796.]

Psammochares (Psammochares) plumbeus (Fabricius); Haupt, 1927: 179. [As type-species of *Psammochares,* after Šustera, 1912.]

Psammochares (Psammochares) plumbeus forma *pulchra* (Fabricius); Haupt, 1927: 181.



Figs 19–31 *Pompilus* species, males. 19–24, head in frontal view of (19) *P. mirandus;* (20) *P. cinereus* (Oriental); (21) *P. cinereus* (Ethiopian); (22) *P. cadmius;* (23) *P. bilineatus;* (24) *P. irpex.* 25, 26, midtarsal claws of (25) *P. cinereus;* (26) *P. bilineatus.* 27–29, antenna of (27) *P. bilineatus;* (28) *P. cinereus;* (29) *P. cadmius.* 30, 31, *P. cinereus* (NW. Europe), (30) SGP; (31) genitalia. Scale lines 19–24, 27–29: 0.5 mm; 25, 26: 0.1 mm; 30, 31: 0.25 mm.

Sericopompilus bivittatus Banks, 1934: 97. LECTOTYPE♀, PHILIPPINES (USNM), here designated [examined]. **Syn. n.**

Psammochares (Psammochares) plumbeus f. *maroccana* Nadig & Nadig, 1935: 10. [Nomen nudum.]

Psammochares plumbeus (Fabricius); Arnold, 1937: 47. [As type-species of *Psammochares;* Ethiopian fauna.]

[*Psammochares latilabris* Arnold, 1937: 47; ♂. Missassociation of sexes. Misidentification.]

[*Psammochares bilineatus* Arnold, 1937: 50; all ♀ of type-series, save holotype. Misidentification.]

Aporoideus clarus Banks, 1941: 359. Holotype ♀, MADAGASCAR (ANS) [examined]. **Syn. n.**

Pompilus plumbeus (Fabricius); Wilcke, 1942: 25.

Pompilus pulcher Fabricius; Wilcke, 1942: 25. [Invalid subsequent designation of type-species for *Pompilus* Fabricius, 1798, in anticipation of Opinion 166.]

Pompilus pulcher Fabricius; International Commission on Zoological Nomenclature, Opinion 166, 1945: 377. [*P. pulcher* validated as type-species of *Pompilus* Fabricius, 1798; all previous designations set aside.]

Pompilus plumbeus (Fabricius); Evans, 1951: 208.

[*Pompilus pulcher* f. *placidus* Priesner, 1968: 176. Unavailable name, proposed expressly for a form.]

Pompilus plumbeus lusitanicus Wolf & Diniz, 1970: 23. Holotype ♀, PORTUGAL (NMW, not 'Narodni Museum, Prag' as originally stated) [examined]. **Syn. n.**

Pompilus cinereus (Fabricius); Evans, 1972: 11.

Pompilus plumbeus gotlandicus Wolf, 1972*a*: 83. Holotype ♀, SWEDEN (NR) [examined]. **Syn. n.**

Pompilus plumbeus chevrieri Tournier; Wolf, 1972*a*: 84.

P. ithonus Cameron. Cameron described female and male; a specimen of each sex in BMNH bears labels 'Pompilus ithonus Cam. type Deesa'. The female is *P. cinereus*, the male *P. mirandus*. I have labelled and here designate as lectotype the female specimen.

S. bivittatus Banks. Banks described only the female, and listed two localities. A female from Iligan, Mindanao in the USNM bears a label in Banks's handwriting, 'Sericopompilus bivittatus Type' and a red USNM type label, no. 51230. A second female, from Cuernos Mts, Negros, bears a USNM paratype label no. 51230. A third female, from Cuernos Mts, in MCZ, bears Banks's paratype label and MCZ label 'Type 17108'. There is also an unlabelled male in USNM. I have labelled, and here designate as lectotype, the female from Iligan, which bears Banks's type label.

P. plumbeicolor Dalla Torre. A single specimen in Vienna can be identified as Saussure's *Ferreola plumbea;* I have labelled it holotype of Dalla Torre's *P. plumbeicolor*.

Haupt (1929: 193) placed *P. cadmius* Saussure in the synonymy of *P. plumbeus*. However, it is here accorded status as a distinct species (p. 29). He also referred to an undescribed species from 'Nyassa-See' which is in all probability either *P. cadmius* or *P. bilineatus*. He also placed *Salius (Schistosalius) atristylus* Saussure, 1892, in the synonymy of *P. plumbeus*. I have not yet been able to locate type-material and cannot place the species on the basis of the figure. However, it is not a *Pompilus*.

Arnold (1937) placed three further names in the synonymy of *P. plumbeus;* Evans (1972) referred to these as possible synonyms of *P. cinereus*. Two of these (*P. pruinosus* Smith, 1879 and *P. sericeibalteatus* Cam.) are here so confirmed. The third, *Pompilus subsericeus* Saussure, is not so; the holotype specimen agrees well with the figure; it is a species of *Anoplius* s. str. (see p. 36). Saussure's description mentions the characteristic spinous setae on the sixth tergum and it is difficult to see how Arnold might have misidentified the species. Evans (1972) quotes Arnold as listing 'China' amongst the localities for *P. plumbeus* (= *cinereus*). This information was doubtless based on the type-locality (Shanghai) given for *P. subsericeus* Saussure. Whilst I have no doubt that *P. cinereus* will be found to be widespread in China, the record is based on a misdetermination. I have seen one Chinese specimen.

♀. Length 5–14 mm. Black, occasionally tending to pinkish red on limbs and tegulae: pubescence grades from uniformly brown-black, through limited amounts of blue-grey to development of an almost entire covering of thick whitish grey pubescence. Wings hyaline or fusco-hyaline, forewing with infuscate outer margin. Calcaria white, stramineous, brown or grey. Temples, prothorax and fore coxae with long, erect white hairs, sterna with few erect dark hairs.

Face broad below, narrowed above, extremely variable (Figs 2, 3) clypeus rarely exceeds 3.2 times as broad as high, margin more or less transverse or convex, labrum almost concealed, not reflexed downwards, slightly indented centrally. Pronotal hind margin angulate, sometimes only weakly so. Postnotum narrowest in centre, but transverse. Propodeum rounded and narrow behind, with a more or less well-developed dorsal longitudinal impressed line. SMC 2 usually much longer than SMC 3 on radial vein, 2nd intercubital cross vein normally sloping, stigma as in Figs 12, 13; sixth tergum with hairs strongly modified as distinct globular leaf-like scales, dark or light in colour, obscuring most of tergum. Fore metatarsus with three comb-spines and two inferior comb-spines, variable in length and thickness. Terminal tarsal segments with row of minute spines beneath; claws dentate or toothless.

♂. Length 4.0–7.5 mm. Black; extensively grey-pubescent, always notably more so than females of similar provenance. Temples with erect white hair.

Head shape variable (Figs 20, 21). Distal antennal segments somewhat thicker than proximal. Propodeum rounded behind, in some populations more abruptly declivous, with a more or less well-defined median sulcus. Wing venation as in female, or with SMC 3 tending to triangular. SGP as in Fig. 30, normally with many erect hairs. Tarsal claws dentate, uniform. Fore metatarsus with two or three comb-spines and one inferior comb-spine, of variable length. Terminal comb-spine often at least half length of second tarsal segment.

P. cinereus is the most widespread species of the genus and through much of its range is the sole *Pompilus* species found. In central and southern Africa, Madagascar and the Orient it is sympatric with various congeners from which it may normally be told by the characters given in the keys. Further notes concerning the identity of its congeners are given under the treatments of those species.

DISTRIBUTION. Throughout the continental Old World including Mediterranean islands, Canary Islands, Madagascar, Sri Lanka, Japan, the Philippines, Borneo, Java and Australia; Maps 1 and 2, pp. 28, 32.

VARIATION. *P. cinereus* is a widely distributed and often common species of perplexing variability both within populations and between them. In a sense, it is here recognized as the residue after definition of its congeners, which are morphologically more stable and of more restricted distribution. Although *P. cinereus* is found from the north-west Atlantic coast of Europe to Australia and from southern Japan to Cape Province, South Africa, I have been able to find no satisfactory criteria for splitting the assemblage into component species. Geographic forms can often be discerned on the basis both of their morphology and colour pattern; however, these forms tend to recur in different parts of the distribution, are probably independently locally derived and are rarely clearly defined when sufficient material is to hand. Nevertheless, it may prove possible in the future to recognize component species within the assemblage.

A feature of *P. cinereus* (and also *P. cadmius*) is the exceptionally large size range encountered, particularly of females, within local populations (see also under 'Biology' p. 17). The phenomenon gives rise to distinct allometric morphological variation. This is most usually observed as a tendency to greater thoracic breadth and depth in relation to length in larger specimens. The face tends also to be relatively narrower between the eyes above in larger specimens. This presents problems in so far as the shape of the face also varies on a geographic basis so as to give an immediate impression of specific distinctness if any two individuals of widely separated populations were to be compared. However, the sum of variation observed points towards clinal trends rather than genetic discontinuity and I feel it premature to attempt any division of the whole on this basis.

A further point of interest lies in the effect of sympatry with its congeners. In Central Africa, *P. cinereus* coexists with two other *Pompilus*, *P. irpex* and *P. cadmius*. *P. cinereus* is most ubiquitous and normally most common of the three; however, the other two are not uncommon species and may be locally abundant. A fourth (rarer) species, *P. bilineatus*, may also coexist with the other three, but less commonly so. Within the boundaries of this coexistence (Map 2, p. 32) *P. cinereus* is remarkably uniform morphologically and with a single colour trend which correlates well with climatic temperature ranges. Beyond this area, *P. cinereus* exhibits a morphological and colour spectrum which approximates to an amalgam of separate characters of the coexistent Central African species, conforming to aspects of the character displacement concept described by Brown & Wilson (1956).

P. cinereus coexists with another congener, *P. mirandus*, in the Oriental region. Here, save in north-west India, *P. cinereus* is less frequent, restricted to sandy shores and river banks. *P. mirandus* on the other hand seems well adapted to more vegetated sandy areas of moderate rain fall, and is often a common pompilid in collections from such regions. Again, where the two species coexist, they adhere well to a defined morphology, though each varies geographically. Beyond the sympatric zone *P. cinereus* approximates more closely to a form intermediate with *P. mirandus;* in north-west India, the two are morphologically very similar and segregate best on characters of the venation and colour pattern. Males are particularly difficult.

Within the range of *P. cinereus,* the following broad trends can be discerned. In north-west Europe and the Cape Province of South Africa, females are extensively black or brown-pubescent balanced with rather little grey or blue-grey pubescence. In hot, dry regions, an entire covering of grey pubescence is developed. In southern India, Saudi Arabia, Cyprus, Mallorca, the Canary

Islands and most of the Sahel region of Africa, grey pubescence predominates, with minimal black coloration, mostly anteriorly on the terga, longitudinally at the sides of mesonotum and the centre of the scutellum. In most other regions, grey pubescence is less than in these extremes, perhaps only 50% of the body surface. However, specimens in poor condition lose pubescence and appear darker than locally is normal. As a general rule, males are never less, usually more, grey-pubescent than females from the same locality. The extent of grey or black pubescence probably correlates with exposure to sunlight; darker individuals are by and large characteristic of colder regions, heavily grey individuals of deserts.

North-west European populations have a relatively broad face and SMC 2 and SMC 3 tend to be approximately equal in area; throughout the remainder of the species range SMC 2 is otherwise much greater in area than SMC 3. Females are predominantly black-pubescent dorsally with narrow transverse strips of grey at the rear of each tergum, interrupted medially. The face is dark above, grey below the antennal insertions. Specimens from Gotland, Sweden, are black with dark brown pubescence posteriorly on the abdomen of some specimens, or with a little grey on that of others; these specimens are the basis of the 'subspecies' *P. plumbeus gotlandicus* Wolf. In northern Spain and Portugal, a dark form (almost identical with that found from Sweden and Poland, via the Low Countries, United Kingdom and France) is found, but with the face narrower above. In southern Portugal, individuals that are almost entirely black are found (*P. plumbeus lusitanicus* Wolf & Diniz), sympatric with more normally grey individuals previously regarded as *P. p. plumbeus*. The latter is characteristic of south-east Spain and the Mediterranean region in general, including North Africa and Morocco. It is worth noting here that previous authors have employed the names *P. pulcher* and *P. plumbeus* for different so-called subspecies of *P. cinereus*, the former supposedly substantially more grey-pubescent than the latter. In fact, the type-material (from Italy and southern Spain respectively) are of similar degrees of grey pubescence!

In the Canary Islands, a grey-pubescent form with white calcaria and a triangular SMC 3 is found. Within the Mediterranean, populations on Mallorca and Cyprus are extremely grey-pubescent, the former with white calcaria. That on Crete, however, is like the north-west European form, save with a narrower face. Israeli material is heavily grey-pubescent but with a narrower clypeus and off-white calcaria.

The dominant African and Madagascan form is similar to that in the Mediterranean, with brown or grey calcaria, face slightly narrower above, and grey colour on head and thorax more uniformly and generally distributed. Only an anterior portion of most terga is black. However, from Ethiopia west across the Sahel to Senegal, including the north of Zaire and the West African coast, a more distinctive form occurs of similar morphology but with white calcaria and pinkish extremities beneath white-grey pubescence. This form is also found eastwards to Saudi Arabia, whilst at Aden and Dhofar, a form of Central African morphology but with a slightly broader face is found. In Cape Province, a form of African morphology but again with a slightly broader face, parallels the dark form of the north-west Palaearctic. Males associated with these females have a more abruptly declivous propodeum. It is this form that Arnold misidentified as his *P. bilineatus*. I have seen forms transitional in colour pattern within a population from Ceres, Cape Province. Mapping of the distribution of the normal African and dark Cape forms would be an interesting project for South African hymenopterists, since there may here prove to be a more abrupt transition than others noted within *P. cinereus*. Both dark and heavily grey-pubescent forms occur on Madagascar.

Across the Palaearctic from Turkey to southern Japan, variation in grey pubescence can be noted, but material is scarce and difficult to interpret. A tendency eastwards to a broadening of the face can also be noted. At Karachi, the females are characterized by a more distinctly brown coloration of the wings. Populations from India become more grey-pubescent and broad-faced, with white calcaria, towards Sri Lanka. From north-west India to Java, *P. cinereus* overlaps the range of *P. mirandus*. However, the two species occur together less frequently than do their congeners in Africa. Forms very close in morphology to the Mediterranean form, but with white calcaria and broader face, have been taken in Burma, Singapore and Java, where in each case they are readily differentiable from the more common and widely distributed *P. mirandus*. Populations are also known from the Philippines and Borneo. However, *P. cinereus* is not common in the

Orient, a probable consequence of the rarity in this region of suitable habitats.

A discontinuity, whether of distribution or of collecting is unclear, exists between Java and Australia, whose populations, of various patterns of grey pubescence, are found from Northern Territory to New South Wales and south west Australia. Australian females have the scales of the sixth tergum confined to a narrower central longitudinal strip than do females from elsewhere in the Old World.

Geographic variation in the form of the male SGP is quite marked. The relative length and thickness of the hair-tufts and the degree of expansion of the lateral transparent portion of the SGP are particularly prone to variation. Extreme differences can often be noted between geographically close populations, but these do not correlate with any noteworthy characters of females.

P. cinereus thus has a distribution which is both land-encompassing in dune systems and on sea shores, both of continents and islands, and dendritic inland, persuing the courses of rivers (both permanent and intermittent). This is uniquely compatible with the kind of all-embracing distribution observed. In particular, the life history is independent of any specific vegetational associations, which for species of other genera may play a decisive part in defining distributions ecologically. For these reasons, coupled with the lack of obvious characters, at least at the level exhibited by its congeners, I treat *P. cinereus* as a single species and thus confirm the view of Evans (1972). Partly for these reasons, I also refuse formally to recognize subspecific entities within the assemblage, and have reduced to synonymy all infraspecific names. However, I also doubt the general value of this traditional approach to taxonomy. I suspect that the system of trinominal nomenclature has served a useful purpose in discouraging the description of spurious species, particularly in popular much-collected groups. However, this historical need should by now be satisfied and we must consider the system *per se.* I see no real need for infraspecific names to be formally recognized within the International Code of zoological Nomenclature, which already positively excludes infra-subspecific names. The fundamental problem is that of endeavouring to utilize binominal nomenclature for functions beyond its practical scope. Problems arise when available infraspecific names must be considered in competition under rules of priority, and each is representative neither of mutually exclusive nor totally inclusive entities. The kind of situation which Betrem (1972: 12) considers is indicative of the inappropriateness of the method. Essentially, I can add nothing to the excellent review by Wilson & Brown (1953) who elected to eschew infraspecific names in their work with Formicidae.

BIOLOGY. A common species particularly of coastal dunes and sandy river beds and banks. The nest is a simple burrow in the sand. The species is noteworthy for forward prey carriage and temporary burial of the prey during nest excavation. Spiders of the families Lycosidae, Gnaphosidae, Zoridae, Clubionidae, Pisauridae and Thomisidae have been recorded from the north-west Palaearctic as prey of *P. cinereus;* see Richards & Hamm (1939), Grandi (1961). Evans & Matthews (1973) record spiders of the genera *Arctosa* and *Pisaura* as prey in Australia. Further records here presented are previously unpublished and include the family Salticidae for the first time; material is in BMNH.

Greece: Ilia, mouth of R. Alfios, 10.vii.1979, *Neatha* sp. (Salticidae), (*M. C. Day*). **Morocco:** Agadir, coastal dunes, 16.v.1975, *Xerolycosa* or *Lycosa* sp. (Lycosidae) (*G. R. Else*). **Tanzania:** Tanga, 19.ix.1917, 2 ♀ each carrying *Lycosa* sp. (Lycosidae) (*W. A. Lambourn*). **Angola:** R. Curoca, 7 m [11 km] NE. of Porto Alexandre, 25.ii.1972, Gnaphosidae (*M. C. Day*). **Botswana:** Lake Ngami, 12 m [20 km] NE. of Sehitwa, 17.iv.1972, *Phlegra* sp. ♂ (Salticidae); Pardosinae (Lycosidae) *(M. C. Day).* **South Africa:** Port Elizabeth, dunes, 27.iii.1953, ?*Lycosa* sp. (Lycosidae); 25.iv.1953, the same (*E. McC. Callan*).

More than two dozen contributions in various languages document observations on the biology of *P. cinereus* (mostly recorded as *P. plumbeus* or *P. pulcher*). Unfortunately, some early authors misconstrued the fragments of behaviour observed. Richards & Hamm (1939), in a summary of the biology of *P. cinereus* (as *plumbeus*) culled largely from the literature but augmented by observation, reported that *P. cinereus* excavates its cells before hunting the prey. In so doing, they accepted in particular the observations of Adlerz (1906). In fact, as previously reported by Stelfox (1927) and subsequently by Mócsár (1943), Crèvecoeur (1945), Bristowe (1948) and Evans & Matthews (1973), the nest is only excavated once the prey has been located and paralyzed.

Unfortunately, Evans (1953*b*; 1958) utilized the incorrect observations in papers synthesizing a schema of behavioural relationships in the Pompilidae. He thus placed *'P. plumbeus'* in a position of unwarranted behavioural evolutionary advancement. This misinformation has unhappily been incorporated in various text books. However, following personal observation of Australian populations, Evans & Matthews (1973) gave information which correlates well with other accounts in which the correct facts were elucidated, which are that the prey is temporarily buried before a burrow is commenced elsewhere. In view of the published dichotomy of opinion, I give further observations of my own. They confirm that *P. cinereus* is behaviourally quite versatile, some apparent inconsistencies between previous reports are thus resolved. I have been able to make original observations with regard to the fate and behaviour of the prey and the development of the larva of *P. cinereus*.

P. cinereus is a common and dominant pompilid in habitats of which the soil is more or less pure sand, often with some proximity to water. In coastal dunes and in sandy river beds and banks throughout the Old World, *P. cinereus* can develop dense populations such that locally it may be the commonest readily observed insect. It exists at much lower densities in more vegetated sandy situations or those which lack the obvious association with water. I have observed it in southern Africa, Greece and South Wales.

In tropical and Mediterranean climates, *P. cinereus* is active notably early in the day. I encountered it at 07.30 at Okahandja, Namibia, considerably earlier than species of other genera would normally be encountered. Similarly, the species was found active as late as 19.30 near Porto Alexandre, Angola. Unless the day was very hot, the species was often found throughout the midday period. Thus, the time available daily for hunting and provisioning was long by comparison with species of other genera. Even in South Wales, *P. cinereus* seems to be active in marginal conditions, when for example *Anoplius infuscatus* or *Arachnospila trivialis* may have ceased activity.

Males of *P. cinereus* are normally to be found flying low over sand in areas where females may be encountered. They are usually small and difficult to net and are thus relatively less frequent in collections than are females. Night and bad weather are passed just below the surface of the sand.

I collected almost three hundred *P. cinereus* in southern Africa (see material examined) but attempted to make biological observations only in Botswana, near Lake Ngami on 17 April, 1972 on the banks of a river south-west of Toteng. *P. cinereus* was very abundant on the gently sloping banks but was not found on the flood plain at any distance from the water. I encountered a female at 10.30 drinking at the waterside, which then flew rapidly to a cattle hoofprint, where she searched for and retrieved a paralysed spider (Pardosinae) of size similar to herself. She picked up the prey in her mandibles, and flew and ran forwards with it for 15 m. Shortly, the top of the slope was reached, and the wasp temporarily buried her prey in a shallow depression, excavated for the purpose in the shade of a leaf of a creeping plant. She then began agitatedly to search hither and thither, until I lost track of her in the general mêlée of active *P. cinereus* individuals. I thus returned to watch the buried prey. After four minutes, a female wasp of identical size approached the prey directly, disinterred it, and set off again. I lost my nerve, and captured it.

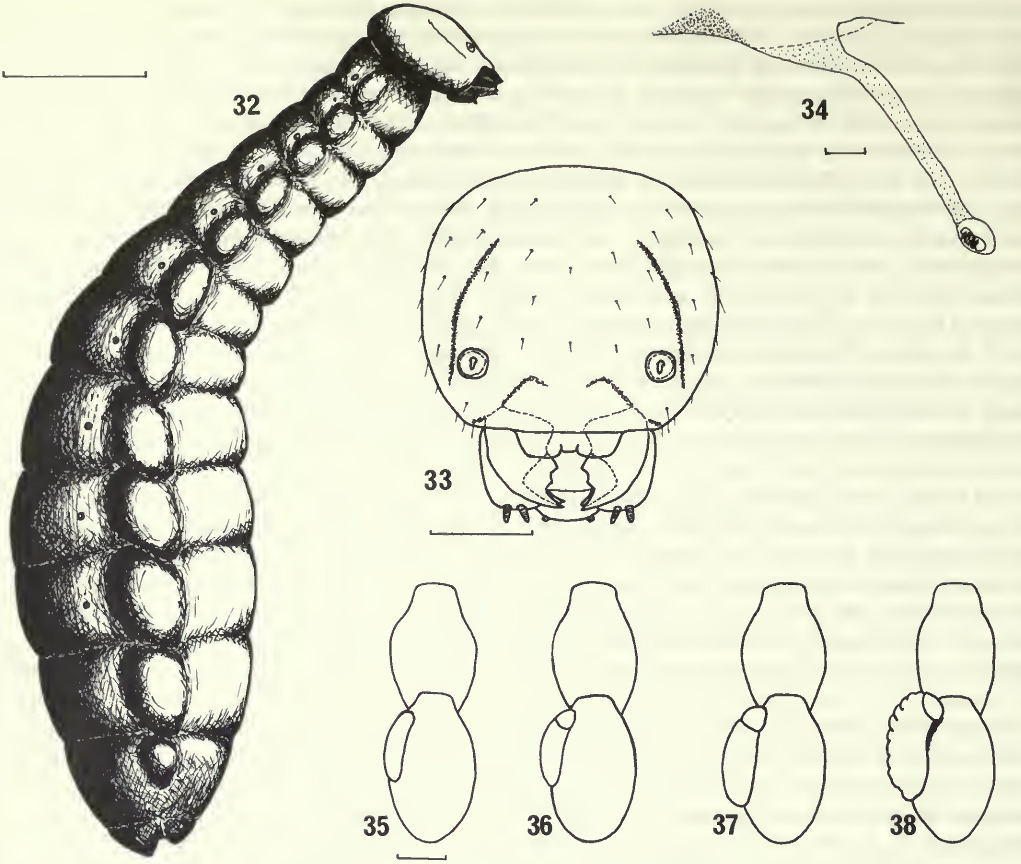
At 12.00 I encountered a female searching by a Malaise trap on soft sand at plain level. She unearthed a temporarily buried prey individual (*Phlegra* sp. ♂). She did not sting it, but ran and flew forwards with it for 5 m, when she effected temporary burial against a lump of compacted sand (the area was much trampled by cattle). She then flew off and searched about for some time until I lost track of her. I waited by the prey, which was revisited twice; on each occasion further sand was kicked over it. After about 15 minutes she disinterred the spider and flew and ran with it directly to a burrow situated at the bottom of a small depression. She ran straight in forwards carrying the spider. Five minutes later the wasp re-emerged and flew off a short distance. I captured the female and excavated the burrow, which was difficult to trace in dry sand. The spider was found at a depth of 8 cm, but bore no egg. Although adding no new knowledge, these observations coincide very closely with those made by Evans & Matthews in Australia, as well as NW. Palaearctic observations.

I have also observed *P. cinereus* in South Wales, on dunes that form part of the Oxwich National Nature Reserve administered by the Nature Conservancy Council. On the 11 August, 1973, on a hot day following heavy overnight rain, Mr G. Else captured a female *P. cinereus* which he realized had been carrying prey. We introduced the female to her prey (*Arctosa perita*) in a glass tube. At 12.55 the wasp picked up the prey by the pedicel, using her mandibles. She was liberated, and proceeded to walk forwards carrying the inert spider. After several hesitant attempts, the prey was temporarily buried in the sand, two legs just protruding, 4 m from the point of liberation. At 13.12, owing to encounters with further females, we lost contact with her. We returned to watch the prey; at 13.21 the prey was recovered by a wasp, moved 2 m east, and reburied. The wasp revisited the prey and scraped more sand over it a minute later. We were able to follow her this time; at 13.28 she began to excavate a burrow at an angle of 45°, the entrance facing towards the sun. Occasionally, the accumulated spoil at the entrance was pushed 2 or 3 cm further back. Digging progressed until the wasp had excavated a burrow which was a little longer than her total body length. The bulk of the medium was damp sand, only a thin surface layer having dried out. At 13.37 she flew off suddenly and was lost. Three minutes later a wasp alighted at the site of prey burial, and 'visited' the prey. At 13.42 a female returned to the burrow and continued excavation. Eight minutes later the wasp left the nest site and returned with the prey after three minutes; it was dropped 10 cm short of the entrance. She inspected the nest, returned to the prey, picked it up and ran straight in head first. Further excavations followed for a minute or so and then the wasp turned round and began scraping material from the walls and roof of the burrow. At 13.57 she flew off and returned. Closure was then completed and the sand in the burrow mouth compacted by hammering with the tip of the abdomen. The surface of the sixth tergum forms the contact surface and is provided with the modified hairs typical of species of the genus. The thorax is held rigid on the legs whilst the abdomen is used as a tamping organ articulating with the propodeum. The abdomen itself moves forwards and backwards and from side to side beneath the thorax, making rapid tamping blows. Internal muscular adjustments modify the length and form of the abdomen as the needs of the work dictate. Finally, the wasp was captured and the nest carefully excavated.

The burrow, about 5 or 6 mm in diameter, proved to slope at approximately 45° for 3 cm, and then descended vertically to a globular cell at a depth of about 7.5 cm in damp sand. The spider bore a glistening white egg, about 1.3 mm long, dorsolaterally on the left anterior face of the abdomen (Fig. 35). Since return to the laboratory was not immediately possible, the prey (which was recovering power of movement) was placed in a dummy cell formed in damp sand contained in a plastic-corked 7.5 × 2.5 cm glass tube. The decision to store the prey in this manner proved fortunate, for when the prey was re-examined at 10.00 on 13th August (44 hours after interrment), it was found to be enclosed in a bag of sand grains, which was of sufficient strength and adhesion to permit the whole to be picked up and suspended. The bag was torn open with forceps and needle; the prey within still bore the intact pompilid egg. The spider was transferred to a solid watch glass provided with a thin layer of sand, and a sheet glass lid so that observations could readily be made. The spider walked about, but without the rapidity expected of normal individuals. Silk was continuously produced from the spinnerets, which in a very short time bound together the sand grains at the substrate surface.

At 14.50 on 14 August the pompilid first instar larva was observed feeding. The surface of the egg that had been cemented to the prey abdomen remained so, whilst the free portion had parted dorsally liberating the larva for an air-breathing existence. However, apart from having penetrated the host integument with the mandibles, permitting the larva to suck in host blood, it had not moved, nor did it do so for some time during its development, until gross-feeding began. At 18.00 the larva had approximately doubled in volume (Fig. 36). By 10.00 of the 15th (Fig. 37) the head was distinct, the gut distended with orange-brown fluid; peristaltic feeding movements were observed. The lateral main tracheae were visible and small fat bodies developing. The third left femur of the spider was close to the larva and made contact when the spider ran, which it could still do in response to substrate-borne vibrations. At 18.00 the spider was still active, though the larva had grown considerably (Fig. 38).

On the morning of the 16 August at 10.00 the spider was moribund. The head of the larve was distinct, with scattered fine setae. Movements of the mandibles were clearly visible in addition to peristaltic movements. The feeding site had been changed from an anterolateral to an anteromedian position on the spider's abdomen. Prey and larva were transferred to a small glass vial so that more



Figs 32–38 *P. cinereus* development. 32, 33, mature larva, (32) right lateral view; (33) head capsule, frontal view. 34, nest and burrow, sectional view. 35, egg. 36–38, early instar larva, (36) 76 hrs from oviposition; (37) 92 hrs; (38) 99 hrs. Scale lines: 32, 34–38: 1.0 mm; 33: 0.25 mm.

complete observation was facilitated and so that an environment of appropriate dimensions was available should the larva survive to spin a cocoon. The larva was of a volume approximately equivalent to that of the shrunken abdomen of the spider. It was attached by its mid venter to the host, on an agglutination of dried host exudate and presumably an indeterminate number of cast larval skins.

At 16.00 the larva had consumed most of this material as a prelude to wholesale consumption of the host. By 23.00 the whole abdomen had been consumed, the larval gut was distended and it contained visible fragments of spider integument. At 09.00 on 17 August the two left rear legs had been eaten. The larva rested on its back and appeared to feed from a (? regurgitated) sludge borne on its own anterior thoracic venter. The remains of the cephalothorax of the host appeared to be held by the abdominal posterior of the larva. Eventually, the larva died without spinning a cocoon, having consumed all save the ventral and anterior faces of the host cephalothorax and appendages.

Three other *P. cinereus* were taken on 11 August with *Arctosa perita* as prey. Capture was observed once: a female pompilid observed a moving *A. perita* on the surface of the sand, rapidly traversed the 0.5 m distance separating them, and immediately grappled with and paralyzed the spider. On many occasions, however, female pompilids were seen to pass within touching distance of *A. perita* individuals which remained motionless and thus apparently undetected. Movement of the prey may be an essential releaser for prey capture on the surface. Bristowe (1948) records that *P. cinereus* individuals seek out *A. perita* individuals in their subterranean tunnels, however.

Following these successful observations, a return was made to Oxwich National Nature Reserve on 17 and 20 August. A female *P. cinereus* was found digging in dry sand near the top of a small partially vegetated dune at 12.50. Five minutes later she retrieved a temporarily buried spider which was carried forwards into the burrow. This sloped at 40°, the entrance facing the sun. At 12.58 the wasp reappeared at the entrance, turned and kicked out loose sand for a minute. A second, smaller, female entered the burrow, re-appeared and re-entered. Both then re-appeared and encountered a third female; all three circled and sparred swiftly, like dogs, for a few moments. The first female then re-entered her nest. Suddenly, at 13.16, the burrow roof collapsed; the female could be seen, partly buried, digging at the sand slip with mandibles and tarsal comb. She attempted a re-excavation, then flew off, investigated nearby burrows, and returned. The sequence was repeated several times until finally she no longer returned. I was unable to find the spider and speculate that the pompilid had not oviposited when disaster struck.

At 14.00 a female was encountered carrying prey. Temporary burial was effected, but the prey was subsequently recovered and re-buried one metre north-west of the original placement. The female was followed for a few minutes but I lost sight of it: I returned to the point at which the prey was buried. A female then arrived and began excavating at the base of a plant, 10 cm from the site of temporary burial. By 14.30 a burrow was completed and the female retrieved the spider. Six cm from the burrow she dropped the prey, inspected the burrow, returned to the spider and ran into the burrow head first. After 35 minutes with no sign of activity, I began excavation. The burrow was blocked at a depth of 3 cm by a thin wall of sand, behind which the pompilid and her prey were sheltering in a small cell. There was no evidence of further excavation, and no egg on the spider (*Cheiracanthium virescens*).

At 15.45 another female was found excavating. At 16.01 she left the nest and flew off several metres. At 16.07 a female appeared near the nest carrying an *A. perita* immature, which was dropped 1 m from the nest. The wasp visited the burrow, then returned for the spider, which was dropped in the nest entrance. She ran round the entrance, then followed the immobile prey inside. At 16.27 the roof of the burrow collapsed near the entrance, leaving a sand bridge. The wasp tore down more sand, executed a few brief 'tamping' movements with the abdomen, and flew off. She was captured and the burrow excavated. The spider was found at a depth of 5 cm directly below the entrance. Unfortunately, a pompilid egg attached anterolaterally on the left of the abdomen was damaged. The spider was placed in a glass vial, in which it soon began to exhibit signs of movement as paralysis wore off.

Since no further pompilid early stages had been secured during the day, the site was revisited on 20 August. At 13.35 a wasp was seen excavating; at 13.50 she flew off and returned with a spider, with which she ran head first into the nest. No spider was subsequently recovered, however. At 14.20 a wasp was encountered carrying prey, which was temporarily buried. I marked the burial site with a pair of sticks placed on the ground at a distance, each pointing towards the spider, intersecting at that point. The pompilid spent much time excavating trial burrows at various places. At 15.03 she returned to her prey, to discover it missing. I had last inspected it at 14.58; in the intervening period, the prey had been removed, most probably by another female *P. cinereus*. The original captor spent several minutes casting about at ever greater distance from the point of interrment, but repeatedly returning unerringly to the exact site of original burial. Eventually, she flew off.

By this date *A. perita* seemed virtually to have been eliminated by the large pompilid population, which increasingly was utilizing *Cheiracanthium virescens* as prey.

A second abortive day seemed likely; in order to salvage something from the time spent, two female *P. cinereus* and two spiders (*C. virescens*) were captured and enclosed in a transparent glass, metal screw-top jar of about 10 cm diameter and 25 cm high. The bottom 8 cm were filled with slightly damp local sand. The *A. perita* individual excavated on 17 August seemed now almost normal in activity, and was also placed in the jar. The pompilid egg it bore was still attached to the abdomen but was flaccid and discoloured. The jar was placed in a bag and transported by car 200 miles to London during the evening. Overnight the bag was left in a darkened room. The jar was removed from the bag only at 09.30 the following morning, on arrival at the BMNH. One of the *C. virescens* individuals was not to be seen anywhere in the jar. The two female pompilids were in cells just below the surface of the sand. One was moribund, but the cell was against the glass; the corpse was recovered. The second female emerged shortly afterwards. She seemed incapable of surmounting the overhang at the neck of the glass jar, and could not fly at a steep angle. Most time was spent in an endeavour to escape towards the window of the room. Accordingly, the blinds were drawn and a 75 watt lamp bulb was mounted to shine vertically downwards directly over the neck of the jar, from which the screw top was removed. Behaviour was altered instantly; the pompilid ran around and across her small arena exactly as in the field, whilst the two spiders remained immobile on the wall of the jar, which was covered by a mat of fine silk. Occasionally, the *Arctosa* (which of course was the individual which had already been used as provision by another pompilid, and still bore the remains of her egg) ventured onto the sand. On a few occasions it was run across by the pompilid, with no apparent reaction from the latter. Observations were interrupted for a period and when resumed at 14.00, the *A. perita* was immobile on its back on the sand, whilst the pompilid had just begun to excavate a burrow adjacent to the glass at an angle of 50–55°. The mandibles were used to loosen grains from the damp sand of the end face of the burrow; the tarsal comb was then employed in removal of spoil to the surface. After a few minutes work, the wasp fetched the spider to the burrow which had been excavated to a depth of 4 cm. Excavation then continued, with spoil being kicked over the prey which was soon 'buried' in the 'floor' of the burrow. At a depth of 8 cm the wasp enlarged the end of the tunnel somewhat to form a single cell (Fig. 34). The spider was then 'unearthed' and dragged into the cell, the wasp walking backwards and pulling on one leg of the spider with its mandibles. For a minute or so, the wasp manipulated the prey, turning it this way and that until finally she allowed it to rest with the head towards the nest entrance, venter down. The wasp adopted a position above the dorsum of the spider's abdomen, facing inwards from the soil surface, and extensively explored the spider's abdomen with its mouthparts. The remains of the previous egg were torn off and discarded or consumed. Eventually, the wasp reversed her position and agitatedly fussed over the prey until the tip of her abdomen was at about the mid-point of the spider's abdomen. She was quiescent for a brief period, then began rapidly to swing the tip of her abdomen back and forth around the upper girth of the prey abdomen, apparently maintaining contact all the while. After a number of such traverses, she ceased with her abdomen on the right-hand side of that of the spider. A few seconds later, she resumed more normal 'neurotic' pompilid behaviour, turning as if to inspect her handiwork. She then commenced immediately to tear at the roof of the burrow and pack the narrow tunnel with sand. When half back-filled, she scooped back material from the spoil heap with her tarsal comb, finally tamping the soil in the manner previously described, using the tip of the abdomen. The tunnel was not filled quite flush with the surface but was left as a shallow depression. By 17.15 the spider had resumed activity and could be seen to bear an egg on the right-hand side of her abdomen. Silk was being produced continuously.

Meanwhile, at 15.30 the remaining *Cheiracanthium* had been overcome and temporarily buried; unhappily, the moment of capture was missed in this instance also. The pompilid had previously encountered the spider, with no apparent reaction, on many occasions. A nest burrow was immediately excavated, on this occasion near the centre of the jar, curving clockwise as depth increased. The spider was recovered and carried in; the tunnel was back-filled and tamped down at 17.15.

On 24 August a first instar larva could be seen feeding on the abdomen of the spider in the cell against the glass. This individual was carefully removed, in its sand-silk envelope, from the sand of the jar. The observations made on the previous larva were repeated, with of course the exception that the feeding position was right antero-lateral rather than left. The larva was fully fed in five days and soon after spun a cocoon in a small glass vial. However, it died before completing the task, the body length about 6 mm, of typical pompilid form (Evans, 1959), with reduced second thoracic spiracle and tridentate mandible (Figs 32, 33).

Previously the rest of the sand had been removed from the container. The *Cheiracanthium* which was observed to have been provisioned was located in a silk-sand cell at a depth of 4.7 cm. The spider was active and bore a first instar pompilid larva antero-laterally on the right-hand side of its abdomen. Unfortunately the larva was injured in the process of excavation, and was thus preserved in alcohol. A third silk-sand cell found at a depth of 6 mm proved to contain the third spider, that which mysteriously had disappeared during transit from original habitat to laboratory! It bore a damaged egg on the right-hand side of the abdomen, but walked out of its cell when the silk lining was torn open. It seems that all phases of behaviour exhibited by the pompilid, hunting, provisioning, ovipositing and cell closure must have taken place at night, without benefit of light, let alone warm sunshine! All three eggs laid by this female had been placed on the right-hand side of the prey abdomen.

These observations and those reported elsewhere may be summarized as follows. *P. cinereus* locates in the sand or encounters on the surface a prey individual which is stung into immobility. The prey is then transported by the wasp, which holds the prey in its mandibles and walks forwards. The prey may be held by pedicel, coxa or spinnerets. Occasionally a small wasp with large prey may need to walk backwards dragging the spider in order to clear an obstacle, after which reversion to forward prey carriage occurs. Large wasps with small prey individuals frequently jump or fly with prey. Most frequently the prey is temporarily interred whilst a suitable nest site is sought and a burrow excavated. Much time may be expended on trial burrows before a site is finally selected. The prey may be inspected or removed to a new site of temporary burial before burrow excavation is completed. When complete, the prey may be brought to the entrance, which is inspected before the prey is carried in, or the wasp may enter directly with prey, either forwards or backwards. Further excavation often takes place before the spider is carried finally into a terminal cell sufficiently large to accommodate wasp and prey. The egg is laid anterodorsolaterally on the prey abdomen. The burrow is then closed, the walls and roof being pulled in by the wasp's mandibles; the cell remains unfilled. Final closure includes more or less tamping of the soil with the tip of the abdomen. The prey recovers from paralysis between 3 and 6 hours after stinging and begins to walk aimlessly about the cell spinning silk continuously. After 3 days, when the wasp first instar is ready to emerge, the spider and wasp egg are contained within a silk-lined cell of considerable structural integrity.

Within these behavioural characteristics must be found most of the parameters which endow *P. cinereus* with the great success in terms of population size which it enjoys in suitable habitats. The production of silk by spiders recovering from paralysis has been recorded by Evans, Lin & Yoshimoto (1953) in the case of *Anoplius apiculatus*. This Nearctic species appears to occupy a niche broadly similar to that of *P. cinereus* in the Old World. Whether a complete cell lining is normally produced, however, is not clear. It seems probable, though I have no positive evidence, that the provision by the prey of such a cell lining is a significant factor in the relative success of *P. cinereus* in its preferred habitat. On the one hand it may serve to prevent collapse of the cell as the sand dries out, as frequently it might do at the shallow depth preferred by the species. Collapse of the cell would probably fatally injure egg or larva. An alternative strategy is exhibited by *Batozonellus fuliginosus* (Klug) which I have observed nesting in Black Cotton soil at Moremi, Botswana. An epeirid prey spider is temporarily suspended on an axil of some convenient leaf a few centimetres above the ground, whilst an initial burrow is excavated. The prey is often visited during this labour, but is eventually carried into the burrow. Further excavation then takes place, the spider is carried to the termination of the burrow and an egg deposited. Soil is then packed tightly around the spider so that it is totally supported by and in contact with sand; no discrete cell is discernible. The burrow is then back-filled and the entrance disguised at the surface. The prey recovered appeared to be deeply paralyzed.

The silk cell lining of *P. cinereus* may on the other hand serve to protect the prey from flooding during periods of rain. I have observed *P. cinereus* in abundance nesting on sandy river beds which had only recently ceased to carry water and which would shortly again do so. Unfortunately I have no evidence of the survival value of the cell lining in this situation. However, it seems likely that the sand-dwelling spiders on which *P. cinereus* preys are themselves adapted to survive periods of inundation protected by the silk linings of their burrows. Whether the lining serves only to maintain the integrity of the structure during flooding or may in some degree be impermeable to water is not clear. It is a very convenient facility for the pompilid to employ, utilising a faculty of the prey, engaged by gentle paralysis from which recovery is rapid. Light paralysis is of course normal in many genera of Pompilidae which construct no nest but leave spiders free-living before they succumb to their ectoparasitic larvae. Whether in the case of *P. cinereus* paralysis of the spider causes its subsequent behaviour to be specifically modified or enhanced, or just marginally inhibited, is an open question.

Other factors probably of significance to the success of *P. cinereus* are its relatively long diurnal periods of activity and its tolerance of diverse climatic conditions. These, combined with behavioural flexibility and versatility, endow the species with many advantages over competitors. The catholic prey preferences (see Richards & Hamm, 1939, and records here quoted) together with acceptance of a wide range of prey size, must also be important. *P. cinereus* (and also *P. cadmius*) exhibit an exceptionally large adult female size range. For example, the largest and the smallest females from a series of *P. cinereus* taken in a single day at a single locality in Greece weighed 20.4 mg and 2.1 mg respectively. A difference in dry weight of virtually ten times is unusual even for species of Pompilidae, all of which so far as is known utilize a single prey individual per egg laid. Such variation is improbable in species of other families which exhibit multiple provisioning and can more readily regulate adult size. This tolerance of prey size is probably a beneficial factor, permitting a greater number of offspring to be left by larger females with no deleterious reduction in number by smaller females. Large females, for example, can readily overcome and transport small spiders which even if too small to succour a larva which will produce a future female can always produce a male individual. Large males are rare in *P. cinereus,* most being no larger than the small 2.1 mg female documented above.

Pompilid eggs, like those of other Hymenoptera, will be female when fertilized, male when not. In the haplo-diploid genetic system, the process of fertilization or its absence is the essential sex-determining criterion. The mechanism *per se* confers the potential for variation of the sex ratio, allowing the placement of eggs of suitable sex in relation to the available food resource. Thus, female eggs can be laid on large spiders and male eggs on small ones. No positive evidence is available to support these particular suggestions for Pompilidae, but the hypothesis accords well with the size distribution of the sexes observed in many long series of *P. cinereus* and with facts adduced for other Hymenoptera such as Ichneumonidae (Arthur & Wylie, 1959; Shaummar, 1966). It is thus quite possible that the sex of the egg of *P. cinereus* is determined in relation to prey size at the time of oviposition. The behaviour earlier described, in which the ovipositing female swings the tip of her abdomen around the contour of the prey abdomen within the cell may well be implicated in stimulating the female to fertilize the egg or to refrain from doing so. Such movements may give a measure of the size of the prey by means of mechanoreceptors detecting the angle at which the pompilid abdomen is deployed. Alternatively, some other part of the process of transport or provisioning may give an indication of total prey body size or weight. However, a mechanism which functions as nearly as possible just prior to the act of oviposition would seem likely to produce the most consistent results. In such a fashion, *P. cinereus* can effectively exploit to the full a wide range of available prey species in various stages of development, both immature and adult.

MATERIAL EXAMINED (1094 ♀, 368 ♂)

Sphex cinerea F., holotype ♀, **Australia** (*Banks*) (BMNH). *Sphex plumbea* F., holotype ♀, **Spain** (UZM). *Pompilus pruinosus* Smith, holotype ♀, **India** (*East India Company*) (BMNH). *Pompilus chevrieri* Tournier, lectotype ♀,**Switzerland**? (MHN). *Pompilus plumbeicolor* Dalla Torre, holotype ♀, **South Africa** (NMW). *Pompilus ithonus* Cameron, lectotype ♀, **India:** Deesa (*C. G. Nurse*) (BMNH). *Pompilus sericeibalteatus* Cameron, holotype ♀, **Tanzania** (*Sjöstedt*) (NR). *Sericopompilus bivittatus* Banks, lectotype ♀, **Philippines:** Mindanao, Iligan (*Baker*) (USNM). *Aporoideus clarus* Banks, holotype ♀, **Madagascar:** north-west, dry region, v.–vii.1938 (*C. Lamberton*) (ANS). *Pompilus plumbeus lusitanicus* Wolf & Diniz, holotype ♀, **Portugal:** Vila Nova di Portimão, 31.vii.1938 (*Zerny*) (NMW). *Pompilus plumbeus gotlandicus* Wolf, holotype ♀, **Sweden:** Farö, Sudersand, 17.vii.1944 (*E. Wieslander*) (NR).

To conform with editorial policy the data of the extensive material examined of this species are presented in an abbreviated form. Countries of W. Europe from which substantial material and published records (as *P. plumbeus*) are available are listed alphabetically without details of material examined. Localities are listed for the remaining parts of the range. Full data are given for specimens from type-series, and the full data of all specimens examined have been deposited in the Entomology Library of the BMNH.

Palaearctic region (345 ♀, 95 ♂)

Algeria: Bône [Annaba]; Biskra; Algiers, Maison Carrée (BMNH). **Austria. Belgium. Canary Islands:**

Fuerteventura, Corralejos; Coti; Lanzarote, Arrecife (BMNH). **Crete:** Georgiopoulis (BMNH). **Cyprus:** Limassol; Akrotiri Bay; Famagusta, Agios Memnos, dunes (BMNH). **Czechoslovakia. Denmark. Egypt:** 'Egypt'; Cairo, gardens and suburbs (BMNH); Assuan (Colln Wahis). **Finland. France. Germany (East). Germany (West). Great Britain. Greece:** Alexandroupolis; Ilia, Olympia, ford; Alfios river mouth; Messinia; Lamia, R. Aspos; Thessalia, Kalambaka; Kalambaka, Pinios riverbed (BMNH). **Hungary. Iran:** Mazanderan, coastal plain between Chalus and Shahsavar (BMNH). **Ireland. Israel:** Palmachin (BMNH). **Italy. Japan:** Osaka, Sumiyshiura; Imaimura, Niigata Pref.; Ryukyu Islands, Ishigakijima, Yarabuzaki (TMU; BMNH). **Libya:** 9 km S. of Tripoli; Tripolitania, Hon Oasis; Sabratha; Gagaresc; Zanzur; Fezzan, Brak (BMNH). **Luxembourg. Mallorca:** Paguera (NMB; BMNH). **Morocco:** Mogador [Essaouira]; Tassida, Souss Valley; Taroudant, Oued Souss; Oued Massa (Tiznit road); Sidi Ifni, coast; Agadir; Tangiers; Tetuan; Melilla, Ixmoart; Sidi Mesand (Colln Wahis; BMNH). **Netherlands. Norway. Poland:** Grabow; Olkusz; Wroclaw; Milicz (Colln Wahis; BMNH). **Portugal. Rumania:** Dobrondja, Constance (BMNH). **Sardinia:** Oristano Tharros (BMNH). **Saudi Arabia:** Jeddah, Haddat, Ash Sham (BMNH). **Sicily:** Selimente (BMNH). **Spain. Sweden:** Fårö, Sudersand, 13–17.vii.1949, 1 ♀, 2 ♂; Gotland, 6.viii.1954, 1 ♀ (paratypes of *P. p. gotlandicus* Wolf) (NR). **Switzerland. Tunisia:** Tozeur; Djerba Island, Ras Torgueness; Tabarka (BMNH). **Turkey:** Kirklarelli Beach, N. of Igneada; Antalya, Kalediran, nr Gazipasa; Sinope; Samsun, Terme; Istanbul, Sile; Kayseri, Sultanhami; Sivas, Koyulhisar; Artvin, 20 km Yusufelli; Mersin, Alata (BMNH). **U.S.S.R.:** Daghestan, Zemeus (Colln Wahis); Kazakhstan, Kaskelen R., 50 km N. of Alma Ata (BMNH). **Yugoslavia.**

Ethiopian and Malagasy regions (560 ♀, 195 ♂)

Angola: Luanda; Lunda, Saurimo; Lunda, Nova Chavez; (CAS); Duque de Bragança Falls; Cachoeiras, 20 m. [32 km] SW. Gabela; Lobito; 12 m [20 km] SW. Luimbale; 5 m. [8 km] NE. Negola; 10 m. [16 km] NE. Cacula; 8 m. [13 km] N.E. Cacula; Sa da Bandeira, Tundavala; Porto Alexandre; R. Curoca, 7 m. [11 km] NE. Porto Alexandre; R. Giraul, 10 m. [16 km] NE. Moçamedes; Roçadas; (BMNH). **Benin Republic:** Malanville (BMNH). **Botswana:** Kuke Pan, 20°59′S, 22°25′E; nr Moremi Reserve, 19°27′S, 23°45′E; L. Ngami, 12 m [20 km] NE. Sehitwa; R. Semowane, 20°25′S, 26°23′E; Palapye; Ngamiland (BMNH). **Chad:** Tibesti, Bardai; Zonar (BMNH). **Ethiopia:** R. Hawash, S. of Adama; Harrar (BMNH). **Ghana:** Labadi (BMNH). **Ivory Coast:** Foro-foro (BMNH). **Kenya:** Marsabit (BMNH); Archer's Post, Uaso Nyiro River; Kwale, Diani Beach (CAS); Tiwi Beach, 40°14′S, 39°36′E (UZM); Usweni, Kitui (Colln Wahis). **Lesotho:** Mamathes (AM; BMNH). **Madagascar:** Tamatave (BMNH); Tananarive (CAS); Sombirano (MNHN); Perinet; Isalo, Km. P. 713; Tulear Prov., St Augustin; Tulear, Beraketa (NHB). **Malawi:** Lingadzi; Domira Bay; Mlanji Boma; Mombera district; valley of Rukuru R.; between Rukuru and Florence Bay: Florence Bay to Karonga; Karonga; between Mvera and L. Nyasa; Mlanje; Shire Valley; Chitala Stream, 10 m. [16 km] W. Domira Bay; Zomba (BMNH). **Mali:** Labbezanga; Gao; Tillembeya (BMNH). **Mozambique:** Beira; Zambesi, Caia (BMNH); Lourenço Marques (Colln Empey). **Namibia:** 32 m. [51 km] SE. Ondangua; Windhoek, Eros Gorge; Swakop R., 3 m. [5 km] S. Okahandja; Okahandja; Khan R., 5 m. [8 km] N. Usakos; Swakopmund (BMNH; UZM); Walvis Bay (BMNH); 2 m [3 km] N. Seeheim (CAS); Gobabeb, Kuiseb R. (UZM). **Niger:** Say; Gaya; Belindi; Niamey (BMNH). **Nigeria:** Maiduguri; Zaria, Samaru; Michika-Bama; 30 m. [48 km] NE. Jos; Bonny; Ibadan (BMNH). **Oman:** W. Rafsah; Dhofar, Ayun Pools (BMNH). **Senegal:** Fatick (BMNH). **Somali Republic:** Senag Plain; Hargeisa (BMNH). **South Africa:** Transvaal, Morenski Dam; T., 5 m. [8 km] N. Warmbad; T., 5 m. [8 km] W. Warmbad (USNM; BMNH); T., Afguns (Hope); T., Letaba Reserve; T., Tshipise; T., Buffelspoort Dam; T., Vaalwater; T., Discovery; T., Ellisras (Colln Empey; BMNH); T., Pretoria North, sandpits (AM); T., Heidelburg (Colln Wahis); Orange Free State, Kroonstad; O.F.S., Chicago, Lindley District (AM; BMNH); O.F.S., Caledon R., Bethulie-Aliwal N. (SAM); Natal, Lake Sibayi (AM); N., St Lucia Estuary (CAS); N., Durban, Stellabush; N., Durban (BMNH); N., Durban, Brighton Beach; N., Reunion Rocks; N., Umbilo; N., Redhill; N., Umhlanga Rocks; N., Umhlali; N., Kloof; N., Escombe (AM; BMNH); N., Movo, N., Winklespruit (TM); N., Weenen, N., Malvern (BMNH); Cape Province, Upington (BMNH); CP., Hartbeespoort Dam (TM); C.P., Lady Grey, 30.xii.1924; 6.i.1925 (3 ♀ paratypes *P. bilineatus*); C.P., Port St John's, Pondoland (BMNH); C.P., Port Alfred, Salt Vlei (AM; BMNH); C.P., Boesman's River, nr Grahamstown (SAM); C.P., Grahamstown, Belmont Valley; C.P., Howison's Poort; C.P., Table Farm; C.P., Hilton (AM; BMNH); C.P., Petersburg, Chunespoort; C.P., Port Elizabeth (NMR; BMNH); C.P., Algoa Bay, (TM; BMNH); CP., Redhouse (NMR); C.P., Zwartkops; C.P., Humansdorp (TM); C.P., Jeffrey's Bay; C.P., Aberdeen; C.P., Beaufort West, Oukloof; C.P., Buffel's R., Ladismith; C.P., 8 m. [13 km] NE. of Touws R. (SAM); C.P., Mossel Bay; C.P., Montagu (BMNH); C.P., Bredasdorp (Colln Empey); C.P., Mordenaars, Karroo (SAM); C.P., Mitchell's Pass, 100 m. [160 km] Cape Town; C.P., Worcester; C.P., Moedverloor, Doorn R. (BMNH); C.P., Namaqualand, Klip Vlei, Garies, x.1931, 2 ♀ (paratypes of *P. bilineatus*); C.P., Hex River, xii.1884, 1 ♀ (paratype of *P. bilineatus*); C.P., Oliphants River between Citrusdal and Clanwilliam, xi.1931, 2 ♀ (paratypes of *P. bilineatus*); C.P., Oliphants River sources; C.P., Cold Bokkefeld; C.P., Bulhoek, Klaver-Clanwilliam; C.P., Citrusdal (SAM);

C.P., Ceres, xi–xii.1920–ii.1921, 35 ♀, 13 ♂ (3 paratype ♀ of *P. bilineatus*); C.P., Witzenberg Valley; C.P., Stellenbosch, iv.1924, 2 ♀ (paratypes of *P. bilineatus*); C.P., Die Panne Nature Reserve; C.P., Cape Town, Milnerton; C.P., Camps Bay, Cape Penin. (BMNH); C.P., Cape Penin., Witsands (NMR). **Southern Yemen:** Aden, Jebel Harir, Wadi Ma'Adin, 50 m. [80 km] WNW. Aden (BMNH). **Sudan:** Hag Zammar (BMNH). **Tanzania:** Kigoma; Tshilinda; Sukh Plains, foot of Sukh escarpment; Tanga; Zanzibar, Pemba Is.; nr Mazi Moja (BMNH). **Uganda:** Entebbe (USNM; BMNH). **Yemen:** Usafira, 1 m. [1.6 km] N. Ta'izz (BMNH). **Zaire:** Uvira; Albertville; Tshiefu, 5°34′S, 23°38′E; Abumombazi (BMNH); 13 m. [21 km] E. of Kenge (CAS); Parc National Upemba, Kasarabilenga, Mabwe, Parc National de Garamba; Musosa (Colln Wahis). **Zambia:** Ft Jameson; Karonga; Luwumbu Valley, Upper Luangwa R.; Upper Luangwa R., Mid-Luangwa Valley; Niamadzi R., Nawalia; Lower Luangwa R.; Luangwa to Petanke; Pakasa; Chirinda Gorge; Lusenfwa; 5 m. [8 km] up Lusenfwa; Chibuyak; SE. of Sjiboda; L. Banguelu, nr Monfuli (BMNH); Lake Mweru, Chiengi (AM; BMNH). **Zimbabwe:** Salisbury, Chishawasha (BMNH); Bulawayo (Colln Empey); Sawmills; Umgusan (NMR); Umtali, ii.1917, 1 ♂ (paralectotype of *P. latilabris* Arnold) (BMNH).

Oriental region (104 ♀, 32 ♂)

Burma: Amherst (BMNH). **China:** Honan, Shanckow (Colln Wahis). **India:** Kashmir; Ranikhet, Kumaon; Deesa (BMNH); Mysore, Nandy Hills; Pondicherry, Karikal (Colln Wahis; BMNH; RNH); Karikal, Kurumbagarum (MCZ; BMNH); Madras, Coimbatore (Colln Wahis; BMNH: RNH); Tranquebar; Nedungadw, Tanjora (MCZ; BMNH); Karnataka, Mudigere; Honavar, sea level (UZM; BMNH). **Java:** W. Java, Mt Salak, 106°46′E, 6°40′S (RNH). **Laos:** Pak Neun (BMNH). **Pakistan:** Karachi (BMNH). **Philippines:** Negros, Cuernos Mts, 1 ♀, 1 ♂ (♀ paralectotype of *S. bivittatus* Banks) (USNM); same data, ♀ (paralectotype of *S. bivittatus*) (MCZ); Negros, Bacolod (RNH; BMNH); Mindanao, Agusan, San Francisco, 10 km SE. (BPBM; Colln Wahis; BMNH). **Sabah:** Papar; Tuaran (BMNH). **Singapore:** Changi; P. Tekong Kechil (BMNH). **Sri Lanka:** Leiden I., Mankuppam; Yala, Palatupana; Palatupana, WLNP Society Bungalow; Anu. district, Wilpattu Natl. Park; Panikka Wila Bungalow; Mannar (USNM; BMNH). **Taiwan:** (BMNH). **West Malaysia:** Negri Sembilan, Port Dickson (BMNH).

Australasian region (85 ♀, 46 ♂)

Australia: Australian Capital Territory, Cotter Res., 10 m. [16 km] W. Canberra; A.C.T., Pine Island Res., 10 m. [16 km] S. Canberra; A.C.T., Murrumbidgee R., near Canberra; A.C.T., Angle Crossing, 20 m. [32 km] S. Canberra (MCZ; BMNH); New South Wales, Bronlee (MCZ; BMNH); Northern Territory, Howard Springs, 16 m. [26 km] E. Darwin; N.T., Tumbling Water, 36 m. [58 km] S. Darwin; N.T., Elizabeth R., 25 m. [40 km] S. Darwin, N.T., Emily Gap, 7 m. [11 km] E. Alice Springs; N.T., Katherine and vicinity (MCZ; BMNH); Queensland, Mackay; Q., Kuranda; Q., Redlynch; Q., Caloundra; Q., Cape York; Q., N. Queensland; Q., Mid-Queensland (BMNH); Q., Yeppoon; Q., Newell Bch, nr Mossman; Q., Magnetic I., off Townsville; Q., Bribie I., 35 m. [56 km] NE. Brisbane; Q., Somerset Down, 70 m. [112 km] NW. Brisbane; Q., 18 m. [29 km] N. Cairns; Q., Coolum; Q., Kuranda and vicinity; Q., Gordonvale; Q., Cunnamulla (MCZ; BMNH); South Australia, Torrens River, near Birdwood, sandbank (MCZ); Western Australia, Flinders Bay (BMNH); W. A., Kununurra and vicinity (MCZ).

Pompilus mirandus (Saussure)

(Figs 1, 14, 19)

Ferreola miranda Saussure, 1867: 49, pl. 3, fig. 30. Holotype ♂ (not ♀ as originally stated), Sri Lanka (MHN) [examined].
Pompilus mirandus (Saussure) Dalla Torre, 1897: 302.
Pompilus ceylonensis Cameron, 1900: 77. Holotype ♀, Sri Lanka (UM) [examined] **Syn. n.**
Pompilus taprobanae Cameron, 1900: 78. Holotype ♀, Sri Lanka (UM) [examined]. **Syn. n.**
Pompilus singaporensis Cameron, 1901: 21. Holotype ♀, Singapore (BMNH) [examined] **Syn. n.**
[*Pompilus ithonus* Cameron, 1908: 301; ♂. Missassociation of sexes; misidentification.]
Pompilus quinquefasciatus Laidlaw, 1938: 11. Holotype ♀, India (RSM) [examined]. **Syn. n.**

F. miranda Saussure. The holotype was thought lost but I found it in a box of miscellaneous Pompilidae in the collections of MHN. It is extensively damaged and glued to a card; the abdomen is lost. However, the specimen is recognizable and agrees with the description. It bears labels 'Type', 'Trincomalee Ceylon', 'Ferreola miranda Ss ♀'; both description and figure-legend also interpret this male specimen as female.

♀. Length 5–13 mm. Black; with more or less extensive grey pubescence at least on antennal pedicel and flagellum, vertex, in front of hind margin of pronotum, centrally and laterally on mesonotum, on scutellum, anterior portions of terga. Forewings hyaline or fuscohyaline, with infuscate outer margin. Calcaria brown or grey. Temples and fore coxae with short erect fine hairs, fewer and shorter than those of *P. cinereus*. Sterna with few erect dark hairs.

Face broader below, narrowed above, more rounded than other species, often roundly produced above tops of eyes (Fig. 1). Clypeus transverse, labrum more or less concealed, not reflexed downwards. Pronotal hind margin angulate, sometimes weakly so, or arcuate. Postnotum transverse, similar to that of *P. cinereus*. Propodeum averaging shorter, squatter than *P. cinereus*, with a dorsal longitudinal impressed line. SMC 2 of forewing longer than SMC 3, second intercubital cross-vein more or less vertical (Fig. 14). Dorsum of sixth tergum with hairs not or only slightly modified as leaf-like scales, when so, only brownish or transparent, rarely obscuring surface of tergum. Fore metatarsus with three comb-spines and two inferior comb-spines; terminal tarsal segments with row of minute spines beneath; claws dentate.

♂ length 4.5–7.5 mm. Black; with more or less extensive grey pubescence, often more so than females from same locality. Temples with erect fine hairs.

Face narrow (Fig. 19). Distal antennal segments not noticeably thicker than proximal, middle segments thickest. Propodeum rounded behind, not strongly declivous, with ill-defined median longitudinal sulcus. Wing venation as female, SMC 3 often tending to triangular. SGP with few erect hairs, otherwise similar to *P. cinereus*. Tarsal claws dentate, uniform. Fore metatarsus with two comb-spines and one shorter inferior comb-spine; terminal comb-spine never exceeds half length of second tarsal segment.

This species has not previously been differentiated from *P. cinereus*, with which it sometimes coexists in the Orient; previous workers have recognized a single species. Most of the names both for *P. mirandus* and *P. cinereus* in this region have been the result of isolated descriptions rather than detailed faunal assessments. The species is morphologically the most generalized of the genus.

Females of the species are readily told when material of both is to hand from a single locality. In Malaya and Java, the shape of the face, the scales of the sixth tergum and the form of the wing venation are diagnostic. However, with some specimens from Sri Lanka, and most from western India, the generally darker appearance resulting from a reduction of grey pubescence and the brown or grey calcaria are more reliable. *P. cinereus* consistently has white or stramineous calcaria throughout the range of *P. mirandus*. Males of *P. cinereus* tend to be more grey pubescent and differ in shape of the face (Fig. 20) from *P. mirandus* males (see below under variation). The *P. mirandus* populations of the Indian subcontinent may eventually prove to be composed of two closely related species.

DISTRIBUTION. Pakistan to Sri Lanka, Burma, Malaya and Java; Map 1, p. 28.

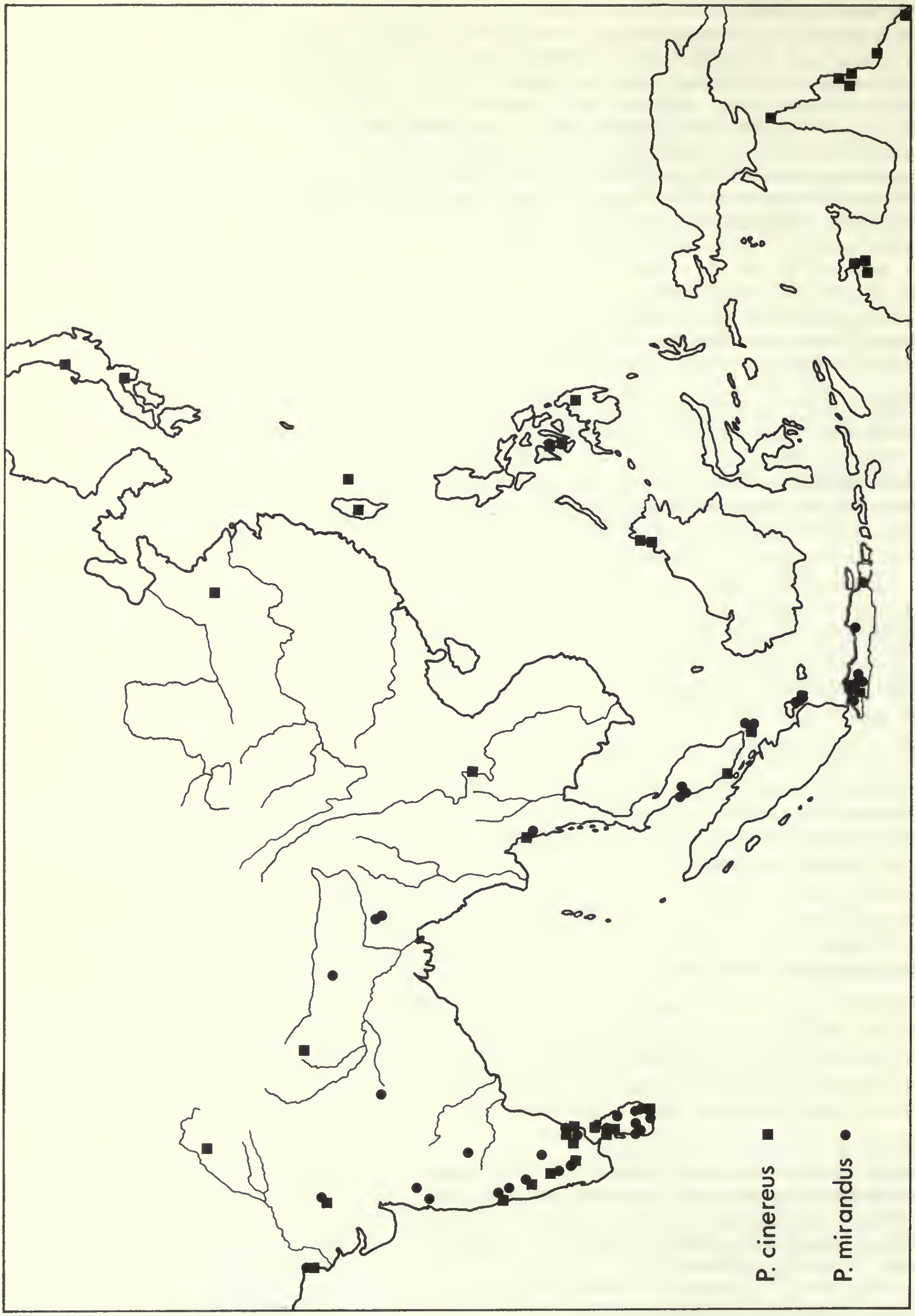
VARIATION. Females in NW. India are morphologically most similar to *P. cinereus*, but in the south and in Sri Lanka they develop the more characteristic shape of face and vertex (Fig. 1). Large individuals are more *cinereus*-like, however. The scales of the sixth tergum are reduced or even like normal pubescence throughout most of the range, particularly in Sri Lanka, Burma, Malaya and Java, though sometimes variable locally. Males are more difficult; the range of variation of *P. cinereus* and *P. mirandus* overlap, such that some individuals may be impossible to place. As stated above, strongly grey-pubescent, broad-faced specimens are placed as *P. cinereus*, less grey-pubescent specimens with narrow face and rounded vertex as *P. mirandus*.

BIOLOGY. No positive information is available. The species is tolerant of more vegetated habitats with higher rainfall than is *P. cinereus*, but is found only in drier forest regions with rainfall of up to 125 or so cm per annum. It is primarily a species of sandy soils, however, as are its congeners. Two of the few records for the genus of capture on flowers; a female taken by J. van der Vecht at Buitenzorg, Java, February, 1935; a male taken by R. L. Coe at Taplejung, Nepal, January, 1962.

MATERIAL EXAMINED (273 ♀, 101 ♂)

Ferreola miranda Saussure, holotype ♂, **Sri Lanka:** Trincomalee (*Humbert*) (MHN). *Pompilus ceylonensis* Cameron, holotype ♀, **Sri Lanka** (*Rothney*) (NM). *Pompilus taprobanae* Cameron, holotype ♀, **Sri Lanka** (*Rothney*) UM). *Pompilus singaporensis* Cameron, holotype ♀, **Singapore:** x.1893 (BMNH). *Pompilus quinquefasciatus* Laidlaw, holotype ♀, **India:** Ranchi Behar, 1928 (*Laidlaw*) (RSM).

Burma: Tenasserim, Amherst Rd, 27–30.xii.1893, 2 ♀ (BMNH). **India:** Assam, Shillong, v.1903, 1 ♀; N. Khasia Hills, 1896, 1 ♀; Deesa, viii.1901–i.1902, 17 ♀, 2 ♂ (1 ♂ paralectotype of *P. ithonus* Cameron); Matheran, iii.1899, 1 ♀; Jubbulpore, v.1907, 1 ♀; Bombay, Nasik, 1 ♀, 2 ♂ (BMNH); Mysore, Nandy Hills, 15.iv.1970, 24 ♀, 11 ♂; Pondicherry, Karikal, i–iv.1962, 10 ♀, 1 ♂; v.1963, 1 ♀ (Colln Wahis; BMNH);


P. cinereus ■
P. mirandus ●

Map 1 Distribution of *Pompilus* species in Oriental and Australasian regions.

iii.1962, 6 ♀ (RNH); Nedungadw, Tanjora, v., 1 ♀, 1 ♂; Coimbatore, 6.ii.1950, 5 ♀ (MCZ); 1934, 1 ♀; 25.ix.-1.x.1979, 1♀ (BMNH); Nilgiri Hills, Gudalur, 3500′ [1060 m], iv.1949, 1 ♀ (MCZ); Karnataka, Mudigere, 900 m, 2–10.xi.1977, 8 ♀, 2 ♂; Honavar, sea level, 24.xi.1977, 3 ♀, 1 ♂; Gersoppa, Jog Falls, 600 m, 19–24.xi.1977, 1 ♀; Bangalore, Allalsandra, 900 m, 26–29.x.1977, 1♀; (UZM; BMNH); Hyderabad, ix–x.1979, 1♀ (BMNH). **Indonesia:** Banka, Mesoel, 9.iii.1931, 1♂; Banka, Aerdingin, 20.ii.1932, 1♀, 1♂; Banka, Batoe Roesa, 28.xi.1935, 1♂; W. Java, Mt Gedeh, 800 m, Tapos, x.1932, 1♀; xi.1932, 2♀; xii.1932, 1♀; 6–11.iii.1933, 1♀; v.1933, 2♀; viii.1933, 1♀; 1–16.viii.1936, 1♀, 8♂; 250 m, Buitenzorg, Tjiboerial, xii.1936–i.1937, 7♀; Gunung Boender, 1.i.1936, 2♀; Buitenzorg, 240 m, on *Borreria latifolia,* 10.ii.1935, 1♀; Buitenzorg, Cultuertuin, 10.ii.1935, 1♀; 700 m, Gunung Megamendoeng, iv–vi.1936, 1♂; Res. Semarang, Djatingalih, vii.1939, 2♀; Niur?, Udjungkulon, 19.vii.1935, 1♂; Malang, Karangpleso, iv.1933, 1♀; Pajut, Preanger, xi.1914, 1♀; Djampang, Tjiajoenan, 100 m, 9.iii.1941, 1♀; Sindanglaja, 1200–1450 m, 3.ix.1934, 1♀; Batavia?, xi.1907, 1♀; Nonkadjadjar, viii.1935, 1♀; Gunung Tjampea, 250 m, 30.iv.1935, 1♀; Bantam, 11.x.1937, 1♀ (RNH, BMNH). **Nepal:** Taplejung District, Dobhan, 3500′ [1070 m], on flowers, 23–31.i.1962, 1♂ (BMNH). **Pakistan:** Karachi, 1.v.1979, 1♀ (BMNH). **Singapore:** Linden Drive (sand), 8.xi.1976, 1♀; P. Tekong Kechil, 24.ix.1967, 1♀ (BMNH). **Sri Lanka:** Hambantota, 12.i.1908, 1♀; 4.x.1908, 1♀; 8.xi.1908, 1♀ (BMNH); Leiden I., Mankuppana, 23.x.1969, 1♀; Mandativu I., 23.x.1969, 6♀, 2♂; Columbo, Museum Garden, 28–31.i.1975, 9♀, 5♂; 15.i.1977, 4♀; 17–23.ii.1977, 3♀, 2♂; 14.vi.1977, 6♀, 1♂; iv.1977, 2♀; Columbo, 11–21.xi.1969, 1 ♀; Katanayaka, near airport, 16.i.1977, 9 ♀; Ratmalana airport, 19–21.i.1975, 7 ♀, 3 ♂; Teledeniya, 11.ii.1975, 1 ♀; Arupola, 27–29.x.1972, 4 ♀, 19 ♂; Uggalkaltota, 10–14.x.1970, 1 ♀; Nugegoda, Papiliyana, 3–4.v.1975, 1 ♀; Kokuwala, 6.vi.1976, 2 ♀; Kandy, Uddawattakele Sanctuary, viii.–ix.1976, 14 ♀, 3 ♂; Katanayaka, Uddawatakele Sanctuary, 30.ix.1976, 4 ♀, 1 ♂; Kandy, Hasalaka, 16–19.ii.1977, 2 ♀; Mon. district, 13 m. [21 km] E. Udawalawe, 16.vi.1976, on sand along Mau Aru, 14 ♀, 3 ♂; Mau Aru, 12 m. [20 km] E. of Udawalawe, 17–19.vi.1976, 3 ♀, 3 ♂; 10 m. [16 km] E. Udawalawe, 24–26.ix.1977, 5 ♀, 1 ♂; Ham. dist., Palatupana, 8–10.iii.1972, 7 ♀, 2♂; 10–12.viii.1972, 2 ♀; 2–6.ii.1975, 5 ♀, 7 ♂, Palatupana Tank, 28.ix.1977, 1 ♀; WLPNS Bungalow, 27–29.ix.1977, 1 ♀, 2♂; Anu. district, Padaviya, 18–21.v.1976, 5 ♀, 2 ♂; Wilpattu Ntnl. Park, Panikka Wila Bungalow, 1.xi.1977, 1 ♀; Hunuwilagana, 22–26.v.1976, 1 ♀; Wilpattu Park, Talawila, 9–10.iv.1973, 1 ♀; Hunuwilagama, Wilpattu, 10–19.ii.1970, 1 ♀; Wilpattu, Mulikulara, Modaragam Aru, 13.vi.1975, 1 ♂; Man. district, Kokmotte Bungalow, 5 m. [8 km] NE. Wilpattu Natl. Park, 21–25.v.1976, 25 ♀, 2 ♂; Mannar, Olaithoduvai, 4–5.xi.1976, 1 ♀; Mannar, Silvatturai and Kondachchi, 24.i.1978, 1 ♀; Kondachchi, Maha, 28.i.1978, 1 ♀; Amp. dist., Panama, 50′ [15 m], Raddela Tank, 14.vi.1976, 14 ♀, 2 ♂; Jaf. dist., 10 m. [16 km] S. Pooneryn, 24–26.i.1977, 1 ♀; Trincomalee, China Bay Ridge, Bungalow, 13–17.v.1976, 1 ♂; China Bay, 27–31.i.1977, 1 ♂; Tennamaravadi, 18.v.1976, 1 ♀ (USNM; BMNH). **West Malaysia:** Perak, Grik. K. Kendrong, 15.i.1962, 2 ♀; Penang, Pantoni Acheh, 26.xii.1958, 1 ♀; Penang, in hotel, 30.x.1960, 1 ♂; Ulu Klang, 25.viii1929, 1 ♀; Dasun Tua, 5.viii.1929, 1 ♀; Serdang, 1 ♂ (BMNH).

Pompilus cadmius Saussure

(Figs 4, 17, 22, 29)

Pompilus cadmius Saussure, 1891: 266. LECTOTYPE ♀, MADAGASCAR (MNHN), here designated [examined].

Pompilus cadmius Saussure; Saussure, 1892: 363, pl. 8, fig. 20.

Psammochares latilabris Arnold, 1937: 47. LECTOTYPE ♀, MALAWI (BMNH), here designated [examined]. **Syn. n.**

P. cadmius Saussure. The original description applies quite well to three conspecific female specimens in MNHN. The largest female bears a label 'Madagascar. Grandid.' above a green label 'Pompilus cadmius Ss ♀ Madag.' in Saussure's handwriting. The second has the left forewing detached and glued to a card; it bears a determination label similar to that of the first specimen. The smallest specimen bears a label 'Madagasc. Grandidier' and again, Saussure's determination label. In 1892, Saussure referred specifically to three females collected by Grandidier. M. Wahis had already labelled these specimens as syntypes, and selected the largest as lectotype. I am in agreement with his selection; I have labelled and here designate as lectotype, the largest specimen.

P. latilabris Arnold. Arnold described from six females and a male from various localities and stated 'Types in the British Museum'. One female, from 'Between Mvera and L. Nyasa', and the male, from Umtali, both bear Arnold's red 'type' labels. A second female, from the Luangwa Valley, bears Arnold's green 'paratype' label, and is in NMR. Forty-eight additional females in the collections of BMNH bear locality labels consistent with the localities cited by Arnold. However, four specimens only of this number each bear a small brown label, 'British Museum', of a kind used in the 1930's to identify Museum material on loan to other workers. I believe these to be the remaining syntypes. The six females are conspecific and belong to the species described below. The male is not conspecific with these females, it is a male of *P. cinereus* F.. I have labelled, and here designate as lectotype, the female specimen labelled 'type' by Arnold.

Pompilus cadmius has previously been regarded as a synonym of *P. cinereus* (as *P. plumbeus*).

♀. Length 6–13 mm. Black; extensively and very uniformly white-pubescent, save black on antennal flagellum and anterior margins of some sterna; posnotum devoid of pubescence. Terminal tarsal segments tending to a brownish colour; calcaria white or stramineous. Wings hyaline or fusco-hyaline, forewings with infuscate tips. With long erect white hairs on temples and adjacent areas of prothorax and fore coxae. Sterna with very few erect black hairs.

Face very broad below, narrowed considerably above, less so in Madagascan and South African specimens (Fig. 4). Malar space well developed adjacent to temples, less so adjacent to clypeus. Clypeus approximately 4.0 times as broad as high, margin slightly arcuate; labrum exposed. Temples well developed. Pronotal hind margin angulate, postnotum laterally about half length of centre of postscutellum, considerably narrowed centrally. Propodeum narrow and rounded posteriorly, with distinct dorsal longitudinal impression in midline. Venation of forewing highly characteristic, SMC 3 higher than SMC 2, second intercubital vein perpendicular, stigma large (Fig. 17). Sixth tergum with hairs very strongly modified as distinct, contiguous globular scales, obscuring most of dorsal surface of tergum, and also extending onto lateral surface. Fore metatarsus with three comb-spines and two inferior comb-spines. Terminal tarsal segments lack spines beneath except a few extremely minute spines proximally in some specimens.

♂ 5–8 mm. Black; extensively and uniformly grey-pubescent, save sometimes dark anteriorly on terga or sterna. With limited erect hair, mostly on temples.

Head broad, face broad (Fig. 22), malar space developed. Distal antennal segments usually markedly thickened. Propodeum rounded in profile, narrow behind, with a well-marked median longitudinal sulcus. Wing venation as female. SGP with few erect hairs. Tarsal claws dentate, uniform. Fore metatarsus with two comb-spines and one much shorter inferior comb-spine.

The female should readily be recognized by the form of the SMCs and of the face and clypeus; also the very uniform grey pubescence and stout globular spines of the sixth tergum which extend to its lateral face. Throughout the range of *P. cadmius, P. cinereus* has brown or grey-pubescent calcaria; thus, the white calcaria of *P. cadmius* are diagnostic. However, in the Sahel region, *P. cinereus* has white or stramineous calcaria. The males are difficult to separate from those of *P. cinereus;* the characters given in the key are adequate, but the species is more easily told when specimens of both species are available for comparison. Males of this species apparently are quite rare in collections.

DISTRIBUTION. Arid and semi-arid regions of South Africa, reaching Katanga and Tanzania; also similar areas of Madagascar; Map 2, p. 32.

VARIATION. Very substantial variation in size of the females occurs, by a factor of eight or ten body volumes. However, the species is otherwise fairly stable morphologically. Females from Madagascar and Cape Province have the upper face between the eyes noticeably wider than do females from the greater part of the range in Africa. The females from Cape Province have less grey pubescence and more strongly fusco-hyaline forewings.

BIOLOGY. Like *P. cinereus* in Africa, this is a species of coastal dunes, sandy beds of intermittent rivers, river banks and lake shores. It co-exists widely with *P. cinereus* and *P. irpex* wherever their ranges are coincident.

A female in the BMNH collected by Silverlock on 21.i.1911 at Pakasa, Zambia, is pinned with its spider prey, tentatively identified by F. R. Wanless as ?*Pisaura* sp. This record is coincident with a similar record for *P. irpex*.

MATERIAL EXAMINED (109 ♀, 13 ♂)

Pompilus cadmius Saussure, lectotype ♀, **Madagascar** (*Grandidier*) (MNHN). *Pompilus latilabris* Arnold, lectotype ♀, **Malawi:** between Mvera and L. Nyasa, 12–21.x.1910 (*S. A. Neave*) (BMNH).

Angola: Porto Alexandre, 25.ii.1972, 1 ♀; 2 m. [3 km] N. of Moçamedes, 29.ii.1972, 1 ♀ (BMNH). **Burundi:** Bujumbura, 20.viii.1975, 1 ♀ (Colln Wahis). **Kenya:** Archer's Post, Ewaso Nyiro R., 2350′

[716 m], 6–12.xii.1969, 1 ♀, 1 ♂ (CAS). **Madagascar:** 2 ♀ (*Grandidier*) (paralectotypes of *P. cadmius* Saussure) (MNHN); Beraketa, 5.xi.1958, 2 ♀ (NMB: BMNH); Behara, iv. 1937, 1 ♀ (Colln Wahis); Tamatave, 1894, 1 ♀ (MNHN); 16.ii.1928, 1 ♂ (Colln Wahis); Bekily, region Sud de l'Ile, xii.1932, 1 ♀, 1 ♂ (MNHN). **Malawi:** between Mvera and L. Nyasa, 12–21.x.1910, 2 ♀ (paralectotypes of *P. latilabris* Arnold); same data, 11 ♀; Mlange, 12.vii.1913, 1 ♀; Karonga, 7–11.vii.1910, 2 ♀ (BMNH). **Namibia:** Onseepkans, Orange River, banks, 8–10.i.1972, 3 ♀; Okahandja, 2–4.ii.1972, 3 ♀; Swakopmund, 6–20.ii.1934, 5 ♀, 4 ♂ (BMNH); Kuis, Fish R., 1170 m, 7.v.1958, 1 ♀ (CAS); Fish River Canyon, 16–22.viii.1958, 5 ♀, 4 ♂ (AM; BMNH). **South Africa:** Natal, Weenan, 2840′ [866 m] i.1924, 1 ♀; N., Zululand, Lower Umhlatuzi River, 4.v.1926, 1 ♀; N., Port St John's, Pondoland, 25–31.iii.1923, 2 ♀ (BMNH); N., Salt Vlei, Port Alfred, 25.i.1959, 1 ♀; N., Umhlanga Rocks, 17.xii.1944, 1 ♀ (AM); Transvaal, western, Ellisras, 6.iv.–19.vi.1962, 6 ♀, 3 ♂; T., Afguns (Hope), 7.xi.1962, 2 ♀; T., north-eastern, Letaba Reserve, 2.xi.1962, 1 ♀ (Colln Empey, BMNH); Cape Province, Moedverloer, Doorn River, 8.x.1975, 2 ♀ (BMNH). **Tanzania:** Kigoma, 17.viii.1931, 1 ♀ (BMNH); Mpala, 21.iii.1954, 1 ♀ (MRAC). **Zaire:** Parc National de Garamba, 16.viii.1957, 2 ♀; Kivu, Uvira, 16–23.iii.1953, 1 ♀, (MRAC); Uvira, 1958, 1 ♀ (USNM). **Zambia:** Pakasa, 23–26.i.1911, 6 ♀ (one with prey); 5 m. [8 km] up Lusenfwa, 20.x.1910, 1 ♀; Upper Luangwa River, 27.vii.–13.viii.1910, 1 ♀ (paralectotype of *P. latilabris*); same data, 13 ♀; Lower Luangwa River, 4–13.ix.1910, 2 ♀; Luwumbu Valley, Upper Luangwa River, 2500–3000′ [762–915 m], 19–26.vii.1910, 6 ♀; Niamadzi River, near Nawalia, 17–22.viii.1910, 1 ♀ (BMNH); Chiengi, Lake Mweru, 31.i.1954, 4 ♀ (AM; BMNH). **Zimbabwe:** 96 m. [154 km] SE. Nuanetsi, 21°55′S, 31°30′E, iv.1961, 2 ♀ (NMR; BMNH); Sawmills, 22.xii.1928, 1 ♀ (NMR).

Pompilus bilineatus (Arnold) **comb. n.**

(Figs 5, 10, 18, 23, 26, 27)

Psammochares bilineatus Arnold, 1937: 50. Holotype ♀, SOUTH AFRICA (TM) [examined].

Arnold (1937) gave good figures of the significant characters drawn from the holotype specimen. However, all other specimens referred to this species by him are in fact misidentifications of the dark-pubescent Cape form of *P. cinereus*. The male has not previously been described.

♀. Length 8–14 mm. Black; extensively grey-pubescent, save black pubescence on antennal pedicel and flagellum, front and vertex, dorso-lateral patch on pronotum. Mesonotum, tegulae and scutellum black, with grey-pubescent lateral patches adjacent to parapsidal furrows, continuing backwards, expanding laterally over scutellum and postscutellum. Most of terga posteriorly and most of sterna grey with black anteriorly; a thin longitudinal line medially is black. Undersides of tibiae and tarsi and distal tarsi dorsally, black. Calcaria brown. Wings hyaline, outer margin of forewing infuscate. Face and fore coxae with few erect hairs, temples with many long erect hairs.

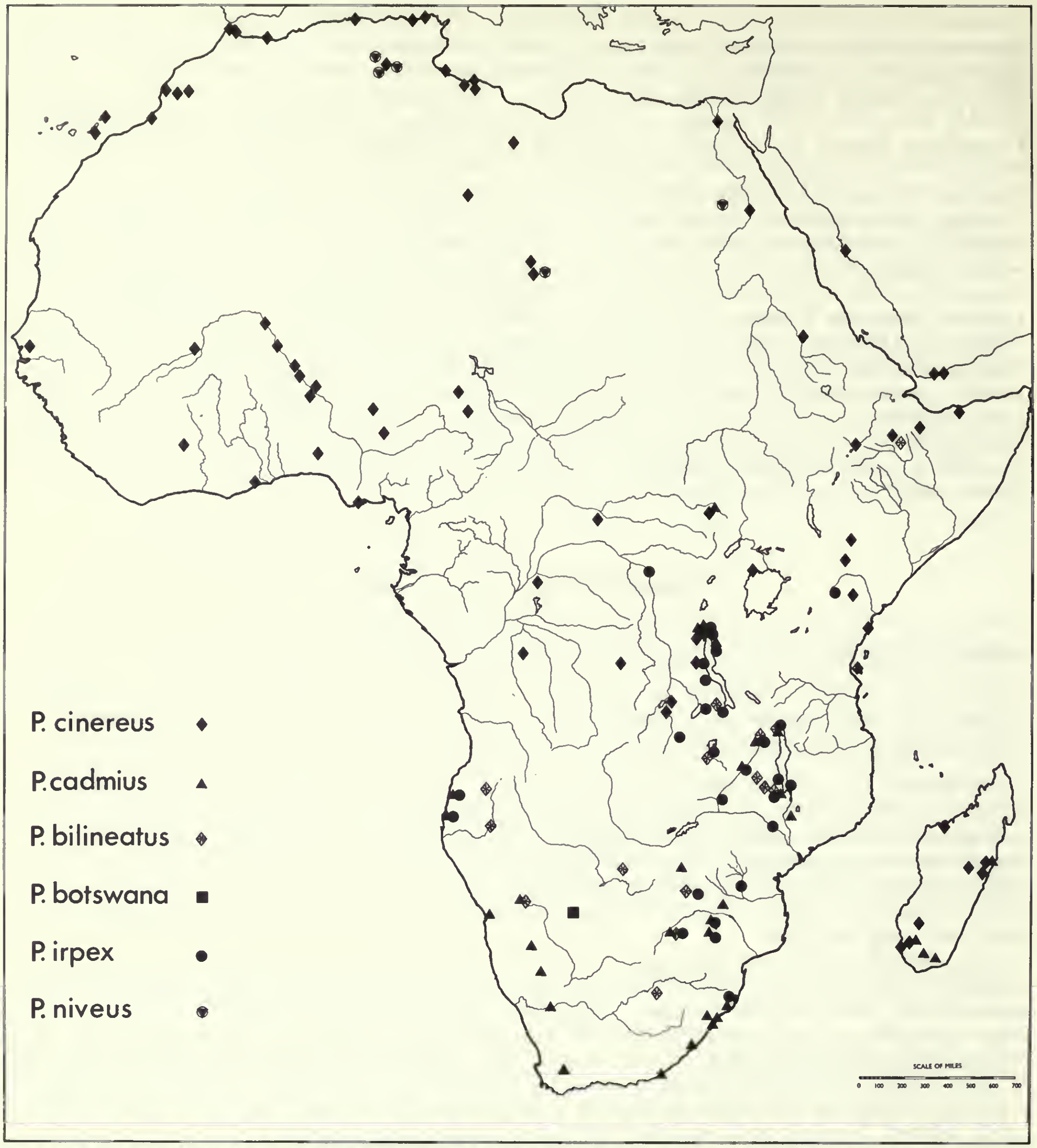
Face relatively high, narrow (Fig. 5), clypeus emarginate, labrum exposed but reflexed downwards towards mouthparts out of plane of clypeus. Pronotum angularly incised, postnotum rather less than half length of postscutellum, little narrowed medially. Propodeum with a well-marked dorsal longitudinal median impression, with a small but distinct, flattened, sloping posterior declivity with flattened corners. Stigma small: forewing venation as in Fig. 18. Dorsal surface of sixth tergum with hairs strongly modified as distinct globular leaf-like scales, black, obscuring most of tergal surface. Fore metatarsus expanded laterally, with three comb-spines and two inferior comb-spines. Apical metatarsal comb-spine distinctly longer than second tarsal segment. Terminal tarsal segments with row of minute spines beneath.

♂. Length 8–10 mm. Black; extensively grey-pubescent, of pattern closely similar to that of female; erect hairs as in female.

Head subquadrate, face narrow, eyes broad, malar space well developed (Fig. 23). Antennal segments tapering distally, not expanded (Fig. 27). Propodeum long, with a definite median sulcus, declivity quadrate and flattened. Forewing venation as female. SGP with very few erect hairs. Tarsal claws of foreleg asymmetric, of others semibifid (Fig. 26). Fore metatarsus with two comb-spines and one inferior comb-spine of similar length.

The female is best recognized by the characteristic forewing venation and the shape of the face, particularly the reflexed labrum. The male claws and antennae render it readily recognizable.

DISTRIBUTION. Kalahari sand through dry Savannah to Ethiopia. This species has on occasion been taken in company with other species of its genus, but is also found well away from the normal habitat of its congeners. It is, however, much more rarely collected; Map 2, p. 32.


P. cinereus ◆
P. cadmius ▲
P. bilineatus ◈
P. botswana ■
P. irpex ●
P. niveus ◉
SCALE OF MILES
0 100 200 300 400 500 600 700

Map 2 Distribution of *Pompilus* species in Africa and Madagascar; *P. cinereus* omitted from central and southern Africa.

VARIATION. The holotype has less grey pubescence than most other specimens seen; however, the species appears morphologically to be very stable, with no readily discernible variation.

BIOLOGY. No information is available for this species.

MATERIAL EXAMINED (27 ♀, 6 ♂)

Psammochares bilineatus Arnold, holotype ♀, **South Africa:** Orange Free State, Bothaville, 18.i.1899 (*H. Brauns*) (TM).

Angola: 10 m. [16 km] NE. of Cacula, 5.iii.1972, 1 ♀; Roçadas, 30.iii.1972, 1 ♀ (BMNH). **Botswana:** near Moremi Reserve, 19°27′S, 23°45′E, 20.iv.1972, 4 ♀ (BMNH). **Ethiopia:** Harar, R. Errer, 20.v. 1948, 1 ♀ (BMNH). **Malawi:** 'Central Angoniland', Lilongwe district, 4000–5000′ [1220–1525 m], 28.v.–2.vi.1910, 1 ♀; Fort Jameson to Dowa, 4000–4500′ [1220–1370 m], 4–9.x.1910, 1 ♀; NW. Shore of L. Nyasa, from Florence Bay to Karonga, 1650′ [500 m], 30.vi.–6.vii.1910, 2 ♀; 'Nyasa', 1901, 1 ♀ (BMNH). **Namibia:** Okahandja, 2–4.ii.1972, 1 ♀, 2 ♂; Swakop River, 3 m.]5 km] south of Okahandja, 7.iv.1972, 1 ♀ (BMNH). **South Africa:** Transvaal, NW., Ellisras, 7.x.1961, 1 ♀; 9.ii.1972, 1 ♀; 31.iii.1972, 2 ♀ (Colln Empey; BMNH). **Tanzania:** near Mazi Moja, 20.viii–ix.1924, 1 ♂ (BMNH). **Zaire:** SE. Katanga, Ngaye, xi–xii.1931, 1 ♀ (MRAC). **Zambia:** Mweru Wantipa, Mushesha, 13–15.i.1954, 3 ♀; Mweru Marsh, Muzombe, i.1955, 1 ♂ (AM: BMNH); Upper Luangwa River, 27.vii–13.viii.1910, 2 ♀, 2 ♂; on road, Fort Jameson to Lundazi, 4000′ [1220 m], 7–14.vi.1910, 1 ♀ (BMNH). **Zimbabwe:** Castle Block, 20°57′S, 27°57′E, 4.iv.1931, 1 ♀ (NMR).

Pompilus botswana sp. n.

(Figs 6, 9)

♀. Length 8 mm. Black; pubescence substantially black, but grey on scapes, lower face and clypeus, temples and occiput, pronotum save a transverse black streak before the posterior margin; with narrow lateral streaks posteriorly on the mesonotum and between parapsidal furrows, expanding posteriorly on the scutellum, postscutellum, and dorsal and posterior surfaces of propodeum. First tergum with extensive lateral patches of grey, second and third with small postero-lateral patches, second and third sterna grey posteriorly; last three segments black. Fore coxa grey ventrally and laterally, mid coxa ventrally, hind coxa ventrally and dorsally. Outer and ventral surfaces of femora grey. For tibia entirely, mid and hind tibiae dorsally, grey. Metatarsi with some grey pubescence, otherwise tarsi black. Calcaria dark. Wings hyaline, outer margin of forewing infuscate. Face and coxae with few sparse, short, erect hairs, temples with many erect white hairs, abdominal venter posteriorly with a few strong erect dark hairs.

Head relatively broad, inner margin of eye strongly sinuous (Fig. 6). Clypeal emargination deep and narrow with a broad polished rim. Hind margin of pronotum angularly incised, Postnotum relatively long, approximately half length of postscutellum, very little narrowed medially. Propodeum elongate, rounded posteriorly in lateral profile, without distinct flattened declivity. Wing venation as for *P. bilineatus* (Fig. 18). Sixth tergum with pubescence strong, the individual hairs much thickened, backwards directed, but not modified to form distinct, globular leaf-like scales, and not obscuring surface of tergum. Fore metatarsus slightly expanded laterally, with three comb-spines, two inferior comb-spines and in addition one shorter spine inserted medio-ventrally between the two rows (Fig. 9). Otherwise like *P. bilineatus*.

♂. Unknown.

This species is closely related to *P. bilineatus*. The relatively unmodified hairs on the sixth tergum and the medial ventral spine on the fore metatarsus readily differentiate it. However, it is also a less robust species than *P. bilineatus*, with much more rich black pubescence, and is subtly different both in the form of the face and of the propodeum.

The trivial name *botswana* is here used as a noun in apposition.

DISTRIBUTION. The unique specimen on which this taxon is based was taken in the Kalahari, in an area from which many currently undescribed endemic species of Pompilidae are known to me; Map 2, p. 32.

BIOLOGY. Unknown.

MATERIAL EXAMINED

Holotype ♀, **Botswana:** 42 miles [67 km] west of Kalkfontein, 11–12.iv.1972 (*M. C. Day: BMNH Southern African Expedition*) (BMNH).

Pompilus irpex Gerstaecker

(Figs 7, 15, 24)

Pompilus irpex Gerstaecker, 1858: 511. Holotype ♀, MOZAMBIQUE (MNHU) [examined].
Pompilus irpex Gerstaecker; Gerstaecker, 1862: 486, pl. 31, fig. 3.
Pompilus pilosus Smith, 1879: 140. Holotype ♀, 'SOUTH AFRICA' (BMNH) [examined]. [Synonymy by Arnold, 1937: 48.]

♀. Length 10–24 mm. Black; sometimes pink on tarsi, extensively grey-pubescent, save black pubescence on antennal pedicel and flagellum; thin anterior band on second and third terga and whole of succeeding terga black. Postnotum devoid of pubescence. Terminal tarsal segments tending to a pinkish ground colour;

calcaria white or stramineous. Wings strongly flavo-hyaline, forewing with infuscate tip. With long erect fine white hairs on face, vertex and temples, on fore coxae; also shorter erect white hairs on thorax. Sterna each with a few strong erect dark hairs.

Face very broad (Fig. 7), malar space well developed, greater than thickness of antenna, clypeus at least 3.5 times as broad as high, arcuate; labrum exposed. Temples strongly developed, frons depressed below anterior ocellus. Pronotal hind margin angulate, postnotum laterally half length of centre of postscutellum, narrowing considerably centrally. Propodeum narrow and rounded posteriorly. Wing venation as in Fig. 15. Sixth tergum with hairs strongly modified as distinct black globular leaf-like scales, obscuring most of surface of tergum. Fore metatarsus with three comb-spines and two inferior comb-spines. Terminal tarsal segments lack spines beneath except proximally in some specimens.

♂. Length 10–14 mm. Black; extensively grey-pubescent, as in female, but terminal abdominal segments also grey, not black; often with more black anteriorly on anterior terga. Much erect fine white hair, as in female.

Head broad, face as in Fig. 24. Malar space developed. Distal antennal segments tapering, as in *P. bilineatus*. Propodeum posteriorly narrowed, but posterior dorsal and lateral angles fairly acute. Wing venation as in female. SGP parallel-sided, with many erect hairs. Terminal segment of fore tarsus mildly asymmetric, fore tarsal claws asymmetric (cf. *P. bilineatus*), others mildly so. Fore metatarsus with three comb-spines, the proximal spine shortest, and one inferior comb-spine at least of length similar to the proximal comb-spine.

This large, yellow-winged species is readily recognized.

DISTRIBUTION. Arid regions and dry savannah from SW. Angola, the Transvaal and Mozambique to Katanga and the Rift Valley lake area of East Africa; Map 2, p. 32.

VARIATION. Little of note.

BIOLOGY. This species, like *P. cinereus* and *P. cadmius* in southern Africa, is a species of lake shores, sandy river beds and banks. It frequently co-exists with the other two species. However, I conjecture that it may be more typically a species of lake sides.

A female in BMNH collected in September by the Oxford Tanganyika Expedition, 1959, at Kasoge Camp, 2550′ [770 m], on the Mahali peninsula, bears a label 'Burrowing on sandy path and dragging one of the large *Arctosa*-type beach spiders'. It is not clear whether forward prey carriage was employed, most probably not when observed. I have found no specimen of prey.

A female collected by Silverlock at Pakasa, Zambia, on 26th January, 1911 has pinned with it as prey an immature lycosid (det. F. R. Wanless). This record coincides with one for *P. cadmius*.

MATERIAL EXAMINED (135 ♀, 13 ♂)

Pompilus irpex Gerstaecker, holotype ♀, **Mozambique:** Tette (*Peters*) (MNHU). *Pompilus pilosus* Smith, holotype ♀, **'Southern Africa'** (*Coll. Chas. Livingstone during Dr D. Livingstone's Expedn*) (BMNH).

Angola: R. Curoca, 7 m. [11 km] NE. of Porto Alexandre, 26.ii.1972, 1 ♀; 2 m. [3 km] N. Moçamedes, 29.ii.1972, 1 ♀ (BMNH). **Burundi:** Rumonga, 800 m, 7.iii.1953, 1 ♀; Bururi, 1948, 1 ♀; Usumbura, 1934, 1 ♀ (MRAC); Bujumbara, plage des Cocotiers, 24.vii.–20.viii.1975, 3 ♀ (Colln Wahis). **Kenya:** Ukumbangi, Nzoi, 1.ii.1889, 1 ♀ (BMNH). **Malawi:** between Mvera and L. Nyasa, 12–21.x.1910, 9 ♀; Karonga, 7–13.vii.1910, 31 ♀, 5 ♂; Chittala Stream, 10 m. [16 km] W. of Domira Bay, 22–28.x.1910, 2 ♀; W. shore of L. Nyasa, between Domira Bay and Kotakota, 29.x.–3.xi.1910, 3 ♀; Lake Nyasa, Domira Bay, 18–21.x. 1910, 1 ♀; Fort Johnston, 2 ♀; Chiromo, 1 ♀; L. Nyasa, Monkey Bay, 20.iv.1915, 1 ♀; Domira Bay, 12.iii.1915, 1 ♀; Lingadzi, near Domira Bay, 9.iii.1915, 1 ♀ (BMNH). **South Africa:** Zululand, Umfolosi River, 23.v.1922, 2 ♂ (BMNH); Transvaal, Gravelotte, Beacon Ranch, i.1966, 1 ♀ (AM); T., north-west, Afguns (Hope), 3.iv.1972, 3 ♀, 3 ♂; T., Ellisras, 6.iv.1962, 2 ♀; 16.xii.1963, 1 ♀ (Colln Empey; BMNH). **Tanzania:** Kigoma, 31.viii.1931, 2 ♀ (BMNH); Kigoma, ix.1918, 6 ♀, 1 ♂ (MRAC); Mahali Peninsula, Lupulunga Ralta, on beach, 31.vii.1959, 1 ♀; Mahali Pen., Kasoge, viii.–ix.1959, 2 ♀, 1 ♂; East Africa (German), 1892?, 1 ♀ (BMNH). **Zaire:** Lunchinda Delta, Lake Mweru, 12.ii.1953, 1 ♀; 3–4.ii.1954, 3 ♀ (AM); Lake Tanganyika, 1 ♀; Kienge, 12.ix.1944, 1 ♀ (Colln Wahis); Baudouinville, 31.iii.1911, 2 ♀; Albertville, 7.ii.1933, 1 ♀; Stanley Falls, 1 ♀ (MRAC); Uvira, 1958, 1 ♀ (USNM). **Zambia:** Pakasa, i.1911, 5 ♀(one with prey); Lusenfwa Gorge, 24.x.1910, 1 ♀; Upper Luangwa River, 27.vii.–13.viii.1910, 9 ♀; Mid-Luangwa Valley, 23–31.viii.1910, 7 ♀; Lower Luangwa River, 4.–13.xi.1910, 9 ♀; near mouth of Lusangazi river, 1–3.ix.1910, 2 ♀ (BMNH); Lake Bangeulu, near Monfuli, 2.x.1946, 3 ♀; Bangeulu District, 1946, 1 ♀; Lake Mweru, Chiengi, 11.i.1953, 2 ♀; 31.i.1954, 1 ♂ (AM). **Zimbabwe:** Sabi River, x.1939, 1 ♀; Gwanda, xi.1965, 1 ♀ (NMR).

Pompilus niveus Saunders

(Figs 8, 16)

Pompilus niveus Saunders, 1901: 549. LECTOTYPE ♀, ALGERIA (BMNH), here designated [examined].
Psammochares (Psammochares) plumbeus forma *nivea* (Saunders) Haupt, 1927: 181.
Chionopompilus rabinovitchi Priesner, 1955: 165. Holotype ♂, EGYPT (El-Azhar University) [not examined]. **Syn. n.**
Pompilus niveus Saunders; Priesner, 1960: 83; ♀.
Chionopompilus rabinovitchi Priesner; Priesner, 1960: 83; ♂. [Suggested possible synonymy with *P. niveus*.]

P. niveus Saunders. Saunders described from five females. Four conspecific females in BMNH agree well with the description and bear compatible locality data. One bears a label 'niveus ES. Type' in Saunders's handwriting. A fifth syntype is housed in MNHN, received as an exchange between Ferton and Saunders. I have labelled and here designate as lectotype, the female bearing Saunders's type label.

C. rabinovitchi Priesner. I have not been able to examine Priesner's holotype, and I have seen no other specimens. However, Mr K. M. Guichard examined the type on my behalf in Cairo during May, 1978. He had with him for comparison females of *P. niveus* and North African *P. cinereus,* and a male of the latter. He is of the opinion that *C. rabinovitchi* is the male of *P. niveus*. Priesner's description (1955) is very detailed; I have summarized only the immediately obvious and useful characters in the following description.

♀. Length 8–11 mm. Black with light extremities; extensively whitish grey-pubescent, very thickly adpressed on head, thorax and abdomen. Postnotum lacks pubescence. Calcaria white or stramineous. Wings hyaline or lightly flavo-hyaline with lightly infuscate tips to forewing. Head, scape, thorax, coxae, femora, tibiae and abdominal venter with profuse fine erect white hairs.

Face as in Fig. 8; clypeus transverse. Labrum exposed, with central arcuate incision. Mandible narrow, sickle-shaped with tooth very much reduced. Malar space as long as antennal segments are thick. Pronotal hind margin angulate or angle arcuately rounded. Postnotum very narrow, narrowest in centre. Propodeum rounded in lateral profile, with slight longitudinal impressed line. Forewing venation as in Fig. 16. Sixth tergum with hairs modified as distinct, white or grey, flat, leaf-like scales, not wholly obscuring the dorsal surface of tergum. Fore metatarsus with three very broad, blade-like comb-spines and at least five inferior comb-spines. Terminal tarsal segments with a row of minute spines beneath.

♂. Length 7.5 mm. Black; tarsi tending to reddish; pubescence much as in female. Body with few erect white hairs. Antennae substantially thicker terminally; fore metatarsus with three lanceolate comb-spines and two inferior comb-spines. Claws simple.

Like *P. irpex,* this is a very distinctive species; it is readily recognized by the tarsal comb and profuse erect hair.

DISTRIBUTION. Sahara Desert; Map 2, p. 32.

VARIATION. The few specimens examined indicate morphological stability over the whole range. Although covering a substantial land area, the habitat is itself probably very stable.

BIOLOGY. Unknown. This species is apparently characteristic of dune systems; it would thus seem to occupy the niche in the Sahara which in the Namib desert is occupied by *Schistonyx atterrimus* Arnold. Many of their morphological specializations are developed in parallel.

MATERIAL EXAMINED (15 ♀)

Pompilus niveus Saunders, lectotype ♀, **Algeria:** dunes, Biskra, 18.v.1893 (*A. E. Eaton*) (BMNH).

Algeria: Biskra, dunes, 17–18.v.1893, 4 ♀ (*A. E. Eaton*) (paralectotypes of *P. niveus*) (BMNH; MNHN); Biskra, 9.iii.1906, 1 ♀ (BMNH); Biskra, iv.1902, 1 ♀ (Colln Wahis); 'Sahara', El Oued, 9.v.1898, 2 ♀; Miaoued Ferzan à M. al Caid, 7.v.1898, 3 ♀; Tillis á Mela, 15.v.1898, 1 ♀; Blidet Ammor á Tillis, 14.v.1898, 1 ♀ (Colln Wahis). **Chad:** Tibesti, Dourzo, 11.iv.1953, 1 ♀ (BMNH).

Additional records. I have not been able to examine the material on which the following records were based by Priesner (1955: 165; 1960: 83). **Egypt:** Gebel Asfar, 12.xi.1933, 1 ♂ (*Rabinovitch*) (holotype of *Chionopompilus rabinovitchi* Priesner) (Al-Azhar University); Gebel Asfar (sand dünen), 30.v.1956, 3 ♀ (*Ali Hafez*) (Ain Shams University) (and NMW?).

Nomenclatural changes in genera other than *Pompilus*

Genus *ANOPLIUS* Dufour

Anoplius Dufour, 1834: 438. Type-species: *Sphex nigerrima* Scopoli, 1763, by subsequent designation (Van der Vecht & Menke, 1968: 120); ratified by ICZN Opinion 997, 1973.

Anoplius subsericeus (Saussure) **comb. n.**

Pompilus subsericeus Saussure, 1867: 60, pl. 3, fig. 39. Holotype ♀, CHINA: Shanghai (NMW) [examined].

Genus *BAMBESA* Arnold

Bambesa Arnold, 1936*b:* 421. Type-species: *Bambesa grisea* Arnold, 1936*b,* by original designation.
Guichardia Arnold, 1951: 178. Type-species: *Guichardia macilenta* Arnold, 1951, by original designation. **Syn. n.**

Bambesa grisea Arnold

Bambesa grisea Arnold, 1936*b*: 422. LECTOTYPE ♂, ZAIRE: Uele, Bambesa, xii.1933 (*H. J. Brédo*) (MRAC), here designated [examined].
Guichardia macilenta Arnold, 1951: 178. Holotype ♂, GHANA: Agogo, 30.i.1942 (*K. M. Guichard*) (BMNH) [examined]. **Syn. n.**

B. grisea Arnold. Described from a female and seven males: I have labelled and here designate as lectotype, a male which agrees with Arnold's figures.

Genus *AMBLYELLUS* **gen. n.**

Type-species: *Pompilus hasdrubal* Kohl, 1894

[*Amblyellus* Wolf, 1965: 29 (as subgenus of *Aporinellus* Banks). Nomen nudum.]
[*Amblyellus* Priesner, 1966*a*: 58. Nomen nudum.]
[*Amblyellus* Priesner, 1966*b*: 200, 206 (as subgenus of *Aporinellus*). Without included species].
[*Amblyellus* Priesner, 1969: 84 (as subgenus of *Aporinellus*). Unavailable under Article 13(b), *Int. Code zool. Nom.*.]
[*Amblyellus* Wolf, 1970: 400 (as genus). Nomen nudum].
[*Amblyellus* Wolf & Diniz, 1970: 12, 23 (as genus). Nomen nudum.]
[*Amblyellus* Wolf, 1972*b*: 130 (as genus). Unavailable under Article 13(b).]
[*Amblyellus* Wahis, 1972: 727 (as genus). Unavailable under Article 13(b).]
[*Amblyellus* Wolf, 1975: 40 (as genus). Nomen nudum.]

The keys of Priesner (1966*b*), Wolf (1972) and the account of Wahis (1972) adequately define the genus.

The following nominal species are assignable to *Amblyellus*; Palaearctic species are listed chronologically, followed by Ethiopian. Specific synonymies are not here established. However, I believe *P. hasdrubal* to be senior available name for the European species currently called *A. obtusus* Gussakowski; whether the latter is a synonym of the former is not clear. Similarly, *P. vegrandis* is probably senior name for a single Ethiopian species.

Amblyellus hasdrubal (Kohl) **comb. n.**

Pompilus hasdrubal Kohl, 1894: 314. Holotype ♂, SPAIN: Barcelona Antiga (NMW) [examined].
[*Aporinellus hanibal* (Kohl) Priesner, 1969:84, 85. Lapsus for *hasdrubal.*]

Amblyellus kiritschenkoi (Gussakowski) **comb. n.**

Sophropompilus kiritschenkoi Gussakowski, 1930: 80. Syntypes 2 ♀, U.S.S.R. (ZI) [not examined].

Amblyellus obtusus (Gussakowski) **comb. n.**

Pompiloides obtusus Gussakowski, 1935: 147. Syntypes 2 ♀, 3 ♂, U.S.S.R. (ZI) [not examined].
Pompiloides insidiosus Nouvel & Ribaut, 1958: 514. Holotype ♀, FRANCE: Bacarès, 22–26.vii.1951 (*P. M. Verhoeff*) (RNH) [not examined]. [Synonymy by Wolf, 1975: 40.]

Amblyellus vegrandis (Kohl) **comb. n.**

Pompilus vegrandis Kohl, 1906: 110. Holotype ♂, SOUTHERN YEMEN: Aden, xii.1898 (*O. Simony*) (NMW) [examined].

Amblyellus willowmorensis (Arnold) **comb. n.**

Psammochares willowmorensis Arnold, 1937: 51. LECTOTYPE ♀, SOUTH AFRICA: Willowmore, 1.i.1902 (*H. Brauns*) (TM), here designated [examined].
[*Amblyellus africanus* Wahis, 1972: 727. Nomen nudum].

Arnold described *P. willowmorensis* from both females and males. I have labelled and here designate as lectotype the female labelled 'type' by Arnold, which agrees with his figures.

Acknowledgements

I am indebted to the following workers who have loaned type- or other material or facilitated visits to collections in their care: Dr P. H. Arnaud, San Francisco: Dr C. Baroni-Urbani, Basle; Dr C. Besuchet, Geneva; Mr F. C. de Moor, Bulawayo; Dr J. Decelle, Tervuren; Mr H. N. Empey, Johannesburg; Dr M. Fischer, Vienna; Mr F. W. Gess, Grahamstown; Dr A. J. Hesse, Cape Town; Dr R. Ishikawa, Tokyo; Dr S. Kelner-Pillault, Paris; Dr E. Königsmann, Berlin; Dr K. V. Krombein & Dr A. S. Menke, Washington; Dr W. W. Moss, Philadelphia; Mr E. C. Pelham-Clinton, Edinburgh; Dr P. I. Persson, Stockholm; Dr B. Petersen, Copenhagen; Mr J. van Reenan, Pretoria; Ms M. Thayer, Harvard; Mr S. C. Willemstein, Leiden; Dr H. V. Daly, Berkeley, loaned material of *Hesperopompilus*. Prof. H. E. Evans (Colorado) and my good friend Mr R. Wahis loaned much material and took much interest in aspects of the work. The Nature Conservancy Council and Mr Methuen Campbell facilitated work at Oxwich National Nature Reserve, Gower Peninsula. Mr F. R. Wanless (BMNH) identified spider prey.

References

Adlerz, G. 1906. Lef nads för hallenden och instinkter inom familjerna Pompilidae och Sphegidae. *K. svenska VetenskAkad. Handl.* **42** (1): 1–48.
Arnold, G. 1932. The Psammocharidae of the Ethiopian region. *Ann. Transv. Mus.* **15:** 41–122.
—— 1934*a*. On three new and remarkable genera of the family Psammocharidae. *Occ. Pap. Rhod. Mus.* **3:** 1–9.
—— 1934*b*. Psammocharidae of the Ethiopian region Part 3. *Ann. Transv. Mus.* **15:** 283–400.
—— 1935. The Psammocharidae of the Ethiopian region. *Ann. Transv. Mus.* **15:** 413–483.
—— 1936*a*. The Psammocharidae of the Ethiopian region. *Ann. Transv. Mus.* **18:** 73–123.
—— 1936*b*. The Psammocharidae of the Ethiopian region. *Ann. Transv. Mus.* **18:** 415–460.
—— 1937. The Psammocharidae of the Ethiopian region. *Ann. Transv. Mus.* **19:** 1–98.
—— 1951. Sphecidae and Pompilidae (Hymenoptera) collected by Mr K. M. Guichard in West Africa and Ethiopia. *Bull. Br. Mus. nat. Hist.* (Ent.) **2:** 97–183.
Arthur, A. P. & Wylie, H. G. 1959. Effects of host size on sex ratio, development time and size of *Pimpla turionellae* (L.) (Hymenoptera, Ichneumonidae). *Entomophaga* **4:** 297–301.
Ashmead, W. H. 1900. Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. *Can. Ent.* **32:** 145–155.
—— 1902. Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. Parts 3 & 4. *Can. Ent.* **34:** 79–88, 131–137.
Banks, N. 1910. New species of Psammocharidae. *Jl N.Y. ent. Soc.* **18:** 114–126.
—— 1912. Psammocharidae: Classification and descriptions. *Jl N.Y. ent. Soc.* **19:** 219–237.
—— 1917. New fossorial Hymenoptera. *Bull. Mus. comp. zool. Harv.* **61:** 97–115.
—— 1934. The Psammocharidae of the Philippines. *Proc. Am. Acad. Arts Sci.* **69:** 1–117.
—— 1938. Some Psammocharidae from Singapore. *Proc. ent. Soc. Wash.* **40:** 236–249.
—— 1941*a*. Some Psammocharidae from Madagascar (Hymenoptera). *Proc. Acad. nat. Sci. Philad.* **92** (1940): 335–362.
—— 1941*b*. Psammocharidae from the Solomon Islands, Prince of Wales Island, and New Caledonia. *Occ. Pap. Bernice P. Bishop Mus.* **16:** 231–245.
—— 1944. Two new genera of Psammocharidae (Hym.) *Psyche* **50** (1943): 82.

—— 1946. Studies of South American Psammocharidae. Part 1. *Bull. Mus. comp. Zool. Harv.* **96:** 311–525.

—— 1947. Studies of South American Psammocharidae. Part 2. *Bull. Mus. comp. Zool. Harv.* **99:** 371–486.

Beaumont, J. de 1946. Les pompilides de la collection H. Tournier – Pompilinae de l'Europe centrale *Mitt. schweiz. ent. Ges.* **20:** 161–181.

Betrem, J. G. 1972. The African Campsomerinae (Hymenoptera, Scoliidae). *Monografieën. Ned. Ent. Ver.* **6:** 1–326, 6 pls.

Bradley, J. C. 1944*a*. A preliminary revision of the Pompilinae of the Americas exclusive of the tribe Pompilini (Hymenoptera: Pompilidae). *Trans. Am. ent. Soc.* **70:** 23–157.

—— 1944*b*. The generic position of certain Mexican Pompilidae (Hymenoptera), with description of a new genus. *Notul. Nat.* **145:** 1–12.

—— 1946. The generic position of nineteen species of West Indian Psammocharidae (Hymenoptera), with descriptions of two new genera or subgenera. *Mems. Soc. cub. Hist. Nat. 'Filipe Poey'* **18:** 123–131.

Bristowe, W. S. 1948. Notes on the habits and prey of twenty species of British hunting wasps. *Proc. Linn. Soc. Lond.* **1947–48:** 12–37.

Brown, W. L. jr & Wilson, E. O. 1956. Character displacement. *Syst. Zool.* **5:** 49–64.

Brullé, G. A. 1833. Insectes: Hyménoptères. *Expédition scientifique de Morée* **3** (1): 326–395.

Cameron, P. 1900. Hymenoptera Orientalia, or contributions to the knowledge of the Hymenoptera of the Oriental Zoological Region. Part IX. The Hymenoptera of the Khasia Hills. Part II – Section I. *Mem. Proc. Manchr lit. phil. Soc.* **44** (15): 1–114.

—— 1901. On the Hymenoptera collected during the Skeat Expedition to the Malay Peninsula 1899–1900. *Proc. zool. Soc. Lond.* **1901:** 16–44.

—— 1908. A contribution to the aculeate Hymenoptera of the Bombay Presidency. *J. Bombay nat. Hist. Soc.* **18:** 300–311.

—— 1910. Fossores. *Wiss. Ergebn. schwed. Exped. Kilimandjaro . . . Meru . . .* **2** (8)7: 197–296.

Coquebert, A. J. 1801. *Illustratio iconographia insectorum quae in museis parisinus observavit et in lucem edidit Joh. Christ. Fabricius* **2:** 47–90, pls 11–20. Reims.

Costa, A. 1859. Imenotteri Aculeati Famiglia de' Pompilidei; *Pompilidea.* (Gen. *Sphex* part. Lin.-Gen, *Pompilus;* Fab. -*Pompilides,* Westw.). *Fauna del Regno di Napoli* **5:** 1–8. Naples.

—— 1887. Pompilidei, Dolicuridei, Scoliidei, Sapigidei, Tiphiidei, e Mutillidei. *Prospetto degli Imenotteri Italiani da servire di prodromo di Imenotterologia italiana.* **3** (2): 171 pp. Naples.

Crévecoeur, A. 1945. Nouvelles observations sur la nidification de *Pompilus plumbeus* F. (Hym. Pompilidae). *Bull. Annls Soc. r. ent. Belg.* **81:** 157–162.

Dahlbom, A. G. 1843. *Hymenoptera Europaea praecipue borealia . . . per familias, genera, species et varietates disposita atque descripta.* **1.** 172 pp. Lund.

—— 1845. *Ibid.* **3:** 353–528. Lund.

Dalla Torre, K. W. von 1897. *Catalogus hymenopterorum hucusque descriptorum systematicus et synonymicus.* **8.** viii + 749 pp. Leipzig.

Day, M. C. 1979*a*. Nomenclatural studies on the British Pompilidae (Hymenoptera). *Bull. Br. Mus. nat. Hist.* (Ent.) **38:** 1–26.

—— 1979*b*. The species of Hymenoptera described by Linnaeus in the genera *Sphex, Chrysis, Vespa, Apis* and *Mutilla. Biol. J. Linn. Soc.* **12:** 45–84.

Dezcourtilz, T. 1825. Mémoire sur un nouveau genre d'insecte de l'ordre des Hémiptères. *Mém. Soc. linn. Paris.* **3:** 293–297.

Dufour, L. 1834. Observation sur une nouvelle espèce d'*Anoplius* qui n'offre qu'un seul ocelle. *Annls Soc. ent. Fr.* **2:** 483–485.

Evans, H. E. 1951. A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Part III. *Trans. Am. ent. Soc.* **77:** 203–340.

—— 1953*a*. The Mexican species of the genus *Pompilus* (Hymenoptera, Pompilidae). *Ann. ent. Soc. Am.* **46:** 529–543.

—— 1953*b*. Comparative ethology and the systematics of spider wasps. *Syst. Zool.* **2:** 155–172.

—— 1958. The evolution of social life in wasps. *In* Becker, E. C. (ed.), *Proc. 10th Int. Congr. Ent.* **2** (1956): 449–458.

—— 1959. The larvae of Pompilidae (Hymenoptera). *Ann. ent. Soc. Am.* **52:** 430–444.

—— 1972. A review of the Australian species of *Elaphrosyron* and *Telostegus,* with notes on other genera (Hymenoptera: Pompilidae). *Breviora* no. 386: 1–18.

—— 1975. A review of *Psoropempula,* a new genus of Australian Pompilidae (Hymenoptera). *Trans. R. ent. Soc. Lond.* **126** (1974): 261–278.

—— 1976. A revision of spider wasps of the genus *Ctenostegus* (Hymenoptera: Pompilidae). *Aust. J. Zool.* Suppl. no. 43: 1–107.

Evans, H. E., Lin, C. S. & Yoshimoto, C. M. 1953. A biological study of *Anoplius apiculatus autumnalis* (Banks) and its parasite, *Evagetes mohave* (Banks) (Hymenoptera, Pompilidae). *Jl N.Y. ent. Soc.* **61:** 61–78.

Evans, H. E. & Matthews, R. W. 1973. Behavioural observations on some Australian spider wasps (Hymenoptera, Pompilidae). *Trans. R. ent. Soc. Lond.* **125:** 45–55.

Fabricius, J. C. 1775. *Systema entomologiae.* (30) + 832 pp. Flensburg & Leipzig.

—— 1787. *Mantissa insectorum sistens species nuper detectas.* **1.** xx + 348 pp. Copenhagen.

—— 1798. *Supplementum entomologiae systematicae.* (4) + 572 pp. Copenhagen.

—— 1804. *Systema Piezatorum.* xiv + 439 pp. Brunswick.

Fox, W. J. 1894. A proposed classification of the fossorial Hymenoptera of North America. *Proc. Acad. nat. Sci. Philad.* **1894:** 292–307.

—— 1901. The proper names of certain genera of Hymenoptera. *Ent. News.* **12:** 267–269.

Gerstaecker, C. E. A. 1858. Übersicht der von ihm [Hrn. Peters] in Mossambique aufgefundenen und von Hrn. Dr Gerstaecker bearbeiten Hymenopteren aus den Familien der Crabronites, Sphegidae, Pompilidae und Heterogyna. *Mber. K. preuss. Akad. Wiss.* **1857:** 509–513.

—— 1862. Hymenoptera. Hautflügler. *In* Peters, W. C. H. (ed.), *Naturwissenschaftliche Reise nach Mossambique auf befehl Seiner Majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgefürt* **5:** 439–526. Berlin.

Gistel, J. N. 1857. Achthundert und zwanzig neue oder unbeschribene wirbellose Thiere. *In: Vacuna oder die Geheimnisse aus der organischen und leblosen Welt* **2:** 515–603. Straubing.

Grandi, G. 1961. Studi di un entomologo sugli Imenotteri superiori. *Boll. Ist. Ent. Univ. Bologna* **25:** 1–659.

Gribodo, G. 1884, Spedizione Italiana nell' Africa Equatoriale; Risultati Zoologici; Imenotteri. *Annali Mus. civ. Stor. nat. Giacomo Doria* **21:** 277–325.

Guérin-Méneville, F. E. 1844. *Iconographie du règne animal de G. Cuvier.* Insectes. **1.** 576 pp. Paris.

Gussakowski, V. 1930. Psammocharidarum species novae (Hymenoptera). 2. *Ent. Obozr.* **24:** 78–85.

—— 1935. Paläarktische *Pompiloides*-Arten (Hymenoptera, Psammocharidae). *Konowia* **14:** 135–150.

Haliday, A. H. 1837. Descriptions of Hymenoptera collected by Capt. King in the survey of Straits of Magellan. *Trans. Linn. Soc. Lond.* **17:** 316–331.

Haupt, H. 1927. Monographie der Psammocharidae (Pompilidae) Mittel-Nord- und Osteuropas. *Dt. ent. Z.* **1926–27:** 1–367.

—— 1929. Weiterer Ausbau meines Systems der Psammocharidae. Mit Beschreibung neuer Gattungen und Arten. *Mitt. zool. Mus. Berl.* **15:** 109–197.

—— 1930. Die Einordnung der mir bekannten Psammocharidae mit 2 Cubitalzellen in mein System. *Mitt. zool. Mus. Berl.* **16:** 673–797.

—— 1937. Beitrag zur Kenntnis der Psammochariden-Fauna Australiens (Spinnenfangende Wegwespen) Subf. Claveliinae Hpt. Trib. Calicurgini nov. *Z. Naturw.* **91:** 121–136.

—— 1949. Das revidierte System der Pompilidae. Dichotomische tabelle einer Hymenopteren-familie. *Beitr. tax. Zool.* **1:** 63–76.

—— 1950. Pompilidae (Hymenoptera Sphecoidea). *Explor. Parc natn. Albert Miss. G. F. de Witte* **69:** 1–63.

—— 1959. Elemente einer systematischen Aufteilung der Macromerinae m. (Hymenoptera – Sphecoidea) Fam. Pompilidae, subfam. Macromerinae. *Nova Acta Leopoldina* **21:** 1–74.

International Commission on Zoological Nomenclature 1910. Opinion 11. The designation of genotypes by Latreille, 1810. *Smithson. misc. Collns* no. 1938: 1–61.

—— 1910. Opinion 32. The type of the genus *Sphex*. *Smithson. misc. collns* no. 1989: 63–88.

—— 1945. Opinion 166. On the status of the names *Pompilus* Fabricius, 1798 and *Psammochares* Latreille, 1796 (Class Insecta, Order Hymenoptera) and the alleged generic name *Pompilus* Schneider, 1784 (Class Cephalopoda, Order Nautiloidea). *Opin. Decl. int. Commn zool. Nom.* **2:** 375–398.

—— 1946. Opinion 180. On the status of the names *Sphex* Linnaeus, 1758, and *Ammophila* Kirby, 1798 (Class Insecta, Order Hymenoptera). *Opin. Decl. int. Commn zool. Nom.* **2:** 569–588.

—— 1954. Opinion 233. Suppression, under the plenary powers, of the name *Octopodia* Schneider, 1784 (Class Cephalopoda), and of certain reported names published by the same author in 1784. *Opin. Decl. int. Commn zool. Nom.* **4:** 275–296.

—— 1980. Opinion 1157. *Sphex viatica* (sic) Linnaeus, 1758 (Insecta, Hymenoptera); designation of lectotype. *Bull. zool. Nom.* **37:** 96–98.

Kirby, W. 1798. *Ammophila,* a new genus of insects in the class Hymenoptera, including the *Sphex sabulosa* of Linnaeus. *Trans. Linn. Soc. Lond.* **4:** 195–212.

Kohl, F. F. 1884. Die Gattungen der Pompiliden. *Verh. zool.-bot. Ges Wien* **34:** 33–58.

—— 1894. Zur Hymenopterenfauna Afrikas. *Annln naturh. Mus. Wien* **9:** 279–350.

—— 1899. Zur Kenntnis neuer gestachelter Hymenopteren. *Annln naturh. Mus. Wien* **14:** 305–316.

—— 1906. *Zoologische Ergebnisse der Expedition der Kaiserlichen Akademie der Wissenschaften nach Südarabien und Sokotra im Jahre 1898–1899.* Hymenopteren. 133 pp., 10 pls. Vienna.

Laidlaw, W. B. R. 1938. *Pompilus quinquefasciatus* sp. nov. from Ranchi, Behar, India. *Entomologist's mon. Mag.* **74:** 11–13.

Latreille, P. A. 1796. *Précis des caractères génériques des insectes, disposés dans un ordre naturel.* xiii + 7–201 pp. Brive.

—— 1802–03. *Histoire naturelle, générale et particulière, des crustacés et des insectes.* **3.** 468 pp. Paris.

—— 1803*a*. *Nouveau dictionnaire d'histoire naturelle.* **18.** 595 pp. Paris.

—— 1803*b*. *Nouveau dictionnaire d'histoire naturelle.* **21.** 571 pp. Paris.

—— 1804–05. *Histoire naturelle, générale et particulière, des crustacés et des insectes.* **13.** 432 pp. Paris.

—— 1809. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita.* **4.** 399 pp. Paris & Strasbourg.

—— 1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides et des insectes: avec un tableau méthodique de leurs genres disposés en familles.* 444 pp. Paris.

—— 1825. *Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique avec l'indication de leurs genres.* 570 pp. Paris.

Leach, W. E. 1815. Entomology. *In Brewster's Edinburgh encyclopaedia* **9:** 57–172. Edinburgh.

Lepeletier de Saint-Fargeau, A. 1831. *Macromeris. Mag. Zool.* **1:** 29–30.

—— 1845. *Histoire naturelle des insectes.* Hyménoptères. **3.** 646 pp. Paris.

Linnaeus, C. 1758. *Systema naturae.* 10th edn. **1.** 823 pp. Stockholm.

Lucas, H. 1851. (Communication.) *Bull. Soc. ent. Fr.* (2) **9:** lxv-c.

Malaise, R. 1937. Fabricius as the first designator and original inventor of genotypes. *Ent. News* **48:** 130–134.

Mócsár, L. 1943. Zur Ethologie der Wegwespen *Psammochares plumbeus, Anoplius infuscatus* und *Episyron rufipes. Zool. Anz.* **143:** 141–152.

Nadig, A. & Nadig, A. 1935. Beitrag zur Kenntnis der Hymenopterenfauna von Marokko und Westalgerien. Zweiter Teil: Scoliidae, Tiphiidae, Mutillidae, Psammocharidae, Chrysididae. *Jber. naturf. Ges. Graubündens* **73:** 3–21.

Nouvel, H. & Ribaut, H. 1958. Trois pompilides nouveaux de la France méridionale (Hymenoptera, Pompilidae). *Bull. Soc. Hist. nat. Toulouse* **93:** 511–518.

Panzer, G. W. F. 1806. *Kritische Revision der Insekten Fauna Deutschlands nach dem System bearbeitet.* (14) + 271 pp. Nuremburg.

Pate, V. S. L. 1946. The generic names of the spider wasps (Psammocharidae *olim* Pompilidae) and their type species. *Trans. Am. ent. Soc.* **72:** 65–130.

Priesner, H. 1955. A review of the Pompilidae of Egypt. *Bull. Soc. ent. Egypte* **39:** 1–208.

—— 1960. Zur Kenntnis der Pompilidae Ägyptens. *Polskie Pismo ent.* **30:** 65–84.

—— 1966*a*. Einiges über Pompiliden (Hymenoptera) (2). *NachrBl. bayer. Ent.* **15:** 57–60.

—— 1966*b*. Studien zur Taxonomie und Faunistik der Pompiliden Österreichs 1. *Naturk. Jb. Stadt. Linz* **1966:** 187–208.

—— 1969. Studien zur Taxonomie und Faunistik der Pompiliden Österreichs. 4. *Naturk. Jb. Stadt Linz* **1969:** 77–132.

Radoszkowski, O. 1888. Révision des armures copulatrices des mâles de la famille Pompilidae. *Bull. Soc. Nat. Moscou* **1888:** 462–493.

Richards, O. W. & Hamm, A. H. 1939. The biology of the British Pompilidae (Hymenoptera). *Trans. Soc. Br. Ent.* **6:** 51–114.

Saunders, E. 1901. Hymenoptera aculeata collected in Algeria by the Rev. Alfred Edwin Eaton, M.A., F.E.S., and the Rev. Francis David Morice, M.A. F.E.S., Part 1. Heterogyna and Fossores to the end of Pompilidae. *Tran. ent. Soc. Lond.* **1901:** 515–563.

Saussure, H. de 1867. Hymenoptera. Familien der Vespiden, Sphegiden, Pompiliden, Crabroniden und Heterogynen. *Reise der Österreichischen Fregatte Novara um die Erde, 1857–1859.* [Zool. Th]. **2:** 1–156. Vienna.

—— 1891. Hyménoptères nouveaux de Madagascar. *Mitt. schweiz. ent. Ges.* **8:** 253–269.

—— 1892. *Histoire physique, naturelle et politique de Madagascar. XX. Histoire naturelles des Hyménoptères* pp. 177–590, pls 21–27. Paris.

Schiødte, J. 1837. Sammenstillung af Danmarks Pompilidae. *Naturh. Tidsskr.* **1:** 313–344.

Shaummar, N. 1966. Anatomie du système nerveux et analyse des facteurs externes pouvant intervenir dans le déterminisme du sexe chez les Ichneumonidae Pimplinae. *Annls Sci. Nat. Zool.* (12) **8:** 391–494.

Smith, F. 1855. *Catalogue of hymenopterous insects in the collection of the British Museum.* Part 3. Mutillidae and Pompilidae. 206 pp. London.

—— 1879. *Descriptions of new species of Hymenoptera in the collection of the British Museum.* xxi + 240 pp. London.

Spinola, M. 1808. *Insectorum Liguriae species novae aut rariores.* **2.** ii + 262 pp. Genoa.

—— 1841. Hyménoptères recueillis à Cayenne en 1839 par M. Leprieur, pharmacien de la Marine Royale. 2e partie. Porte-aiguillons (1). *Annls Soc. ent. Fr.* **10:** 85–149.

Stelfox, A. W. 1927. A list of the Hymenoptera Aculeata (sensu lato) of Ireland. *Proc. R. Irish Acad.* **37**(B): 201–355.

Stephens, J. F. 1827. *Illustrations of British entomology. Mandibulata* **1:** 61–68 (1st November, 1827). London.

Šustera, O. 1912. Die Paläarctischen Gattungen der Familie Psammocharidae (olim Pompilidae, Hym.). *Verh. Zool.-bot. Ges. Wien* **62:** 171–213.

Tournier, H. 1889. Hyménoptères. Étude de quelques pompilides d'Europe et contrées limitrophes. *Entomologiste genèv.* **1889:** 133–140, 154–178.

Townes, H. K. 1957*a*. Nearctic wasps of the subfamilies Pepsinae and Ceropalinae. *Bull. U.S. natn. Mus.* **209:** 1–286.

—— 1957*b*. The name *Psammochares* versus *Pompilus*. *Syst. Zool.* **6:** 151–155, 192.

—— 1969. The genera of Ichneumonidae, Part 1. *Mem. Am. ent. Inst.* **11:** 1–300.

—— 1973. The type of *Sphex viatica* Linnaeus (Hymenoptera, Sphecidae). *Polskie Pismo ent.* **43:** 91–96.

Wahis, R. 1972. Nouvelle contribution à la connaissance de Hyménoptères Pompilides de la Yougoslavie (Hymenoptera: Pompilidae). *Bull. Rech. agron. Gembloux* **5** (1970): 709–744.

Wilcke, J. 1942. Het geslacht *Pompilus* F. (*Psammochares* Latr.). *Ent. Ber., Amst.* **11:** 23–32.

Wilson, E. O. & Brown, W. L. Jr 1953. The subspecies concept and its taxonomic application. *Syst. Zool.* **2:** 97–111.

Wolf, H. 1965. Systematisches Verzeichnis der Wegwespen (Hym. Pompiloidea) Mittel- und Nordeuropas. *Nachr. naturw. Mus. Aschaffenb.* **72:** 1–38.

—— 1970. Wegwespen aus dem Museo Civico di Storia Naturale in Mailand. *Atti Soc. ital. Sci. nat.* **110:** 391–417.

—— 1972*a*. Nachtrag zum Catalogus Insectorum Sueciae, Hymenoptera: Pompiloidea. *Ent. Tidskr.* **93:** 83–87.

—— 1972*b*. *Insecta Helvetica.* Fauna 5. Hymenoptera Pompilidae. 176 pp. Zurich.

—— 1975. Über einige Wegwespen (Hymenoptera, Pompilidae) aus dem Rijksmuseum van Natuurlijke Historie zu Leiden. *Zool. Meded. Leiden* **49:** 27–55.

—— 1978. Systematik, Morphologie und Verbreitung der west-paläarktischen Arten der Wegwespen-Gattungen *Nanoclavelia, Pedinpompilus* und *Agenioidevagetes* (Hymenoptera: Pompilidae). *Entomologie gen.* **5:** 85–103.

Wolf, H. & Diniz, M. de A. 1970. Wegwespen (Hym. Pompil.) aus dem Zoologischen Museum der Universität Coimbra. *Mems Estud. Mus. zool. Univ. Coimbra* **311:** 4–26.

Index

Invalid names are in *italics*.

africanus 37
Amblyellus 9, 36
Anoplius 36

Bambesa 8, 36
bilineatus 10, 12, 13, 31
bivittatus 13
botswana 10, 33

cadmius 10, 12, 14, 29
ceylonensis 26
chevrieri 12
Chionopompilus 7
cinereus, 10, 12
clarus 13

gotlandicus 14
grisea 36
Guichardia 8, 36

hanibal 36
hasdrubal 36

insidiosus 36
irpex 10, 12, 33

ithonus 12, 26
kiritschenkoi 36
latilabris 13
leprosus 12
lusitanicus 14
macilenta 36
maroccana 13
mirandus 10, 12, 26
niveus 10, 12, 35
obtusus 36
pilosus 33
placidus 14
plumbeicolor 12
plumbeus 12
Pompilus 7
pruinosus 12
pulcher 12
quinquefasciatus 26
rabinovitchi 35
sericeibalteatus 12
singaporensis 26
subsericeus 14, 36
taprobanae 26
vegrandis 37
willowmorensis 37

British Museum (Natural History) Publications

Catalogue of the Diptera of the Afrotropical Region

Editor: R. W. Crosskey. *Assistant editors:* B. H. Cogan,
P. Freeman, A. C. Pont, K. G. V. Smith and the late H. Oldroyd.
British Museum (Natural History). 1980, 1437 pp. £55·00

The Diptera or two-winged flies are probably the most important insects that affect man. Although most flies are harmless, some have become transmitters of dangerous diseases to man and his domestic animals, and others are important pests of agricultural crops. Some flies are beneficial because they destroy large numbers of plant-feeding insects through their parasitic or predacious habits.

Nowhere is their socio-economic and medical impact more sharply felt than in tropical Africa, where fly-borne diseases are not only a direct health hazard but can prevent or hinder development of the land. The control of such diseases as sleeping sickness and onchocerciasis depends in great measure upon controlling the flies that carry them. This in turn requires a thorough appreciation of all that is known about the insect vectors, including their basic taxonomy, so that they can be correctly identified and their geographical ranges accurately established.

This catalogue synthesizes the scattered basic taxonomic work on the Diptera of tropical Africa and its islands by listing the known 16,500 species with their synonyms and known geographical ranges within a comprehensive classification. A short introduction is given to each family and a bibliography of 4,700 titles provides references to the primary literature. Such a task has never before been attempted for the region and its completion should greatly stimulate taxonomic research. The *Catalogue* represents ten years' careful work by a team of forty specialists, under the editorship of six dipterists on the staff of the Natural History Museum, themselves contributors with considerable expertise in the African fauna.

The *Catalogue* should serve for a long time as an indispensable tool to the taxonomist and an essential source-work to anyone concerned with African flies in the fields of medical, agricultural and veterinary science.

Titles to be published in Volume 42

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. By Michael C. Day.

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. By Barry Bolton.

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). By J. Mark Ritchie.

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). By Angoon Lewvanich.

Printed by The Whitefriars Press Ltd, London and Tonbridge

BRITISH MU
GENERA
- 3 MAR
LIBRAR
NATURAL H

Bulletin of the
British Museum (Natural History)

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region

Barry Bolton

Entomology series
Vol 42 No 2

26 February 1981

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Ent.)

© Trustees of the British Museum (Natural History), 1981

ISSN 0524–6431

Entomology series
Vol 42 No 2 pp 43–81

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 26 February 1981

BRIT
GENERAL
- 3 MAR 1
LIBRARY
RAL HI

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region

Barry Bolton

Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

- Synopsis . . . 43
- Introduction . . . 44
- Measurements and indices . . . 46
- Abbreviations of museums . . . 46
- *Meranoplus* F. Smith . . . 46
  - Diagnosis of worker . . . 47
  - Synonymic list of species. . . . 47
  - Key to species (workers). . . . 48
  - The species-groups . . . 48
    - The *spininodis*-group . . . 49
    - The *nanus*-group . . . 51
    - The *magrettii*-group . . . 54
- *Dicroaspis* Emery . . . 56
  - Diagnosis of worker . . . 56
  - Synonymic list of species. . . . 58
  - Key to species (workers). . . . 58
  - Treatment by species . . . 58
- *Calyptomyrmex* Emery . . . 59
  - Diagnosis of worker . . . 59
  - Synonymic list of species. . . . 60
  - Key to species (workers). . . . 61
  - The species-groups . . . 62
    - The *barak*-group . . . 62
    - The *piripilis*-group . . . 63
    - The *arnoldi*-group . . . 66
    - The *brunneus*-group . . . 69
- Acknowledgements . . . 75
- References . . . 75
- Index . . . 81

Synopsis

The genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery are revised for the Ethiopian zoogeographical region. Keys to workers of each genus are presented. Eight species of *Meranoplus* are recognized, one of which is described as new; 12 new synonyms are established in this genus, mostly of infraspecific forms, and new status as a valid species is given to one form. *Calyptomyrmex* has 16 species in the fauna. Of these 7 are described as new and 6 synonyms are established. *Dicroaspis* is returned to generic status, with *Geognomicus* included as a new junior synonym; two species are recognized and one new synonym is established.

Bull. Br. Mus. nat. Hist. (Ent.) **42** (2): 43–81

Issued 26 February 1981

Introduction

The three genera treated in this paper have not previously been revised for the Ethiopian zoogeographical region. The species of southern Africa were reviewed by Arnold (1917; 1926) but all other information is included in the scattered literature of original descriptions.

Of the three genera *Dicroaspis* is restricted to central Africa, but *Calyptomyrmex* and *Meranoplus* are both widely distributed in the Old World tropics, ranging through the Oriental and Indo-Australian regions to Australia. The *Calyptomyrmex* species of the Oriental and western Indo-Australian regions have recently been revised by Urbani (1975), but no work has been done on *Meranoplus* to the present.

The maximum number of species of *Calyptomyrmex* occur in Africa, the numbers falling off in an easterly direction, whilst the reverse is true of *Meranoplus* which has its strongest representation in Australia. In terms of numbers of described species, and ignoring infraspecific forms and synonyms, the distributions break down as follows.

	Dicroaspis	*Calyptomyrmex*	*Meranoplus*
Ethiopian region	2	16	8
Malagasy region	–	–	2
Oriental region	–	4	7
Indo-Australian region	–	4	9
Australian region	–	1	21
Totals	2	25	47

The taxonomic histories of *Calyptomyrmex* and *Meranoplus* have been fairly straightforward since their inception, but *Dicroaspis* has had a rather more chequered career. When first described by Emery (1908) it was treated as a valid genus, but later he changed his opinion (Emery, 1915) and from then on he regarded *Dicroaspis* as a subgenus of *Calyptomyrmex;* it was also treated as such by later authors and cataloguers (Wheeler, 1922). The present study reverses the 1915 decision as I am now convinced that *Dicroaspis* deserves generic status, separate from *Calyptomyrmex,* for the reasons given in the discussion of the genus.

The obscure monotypic genus *Geognomicus,* stated at its inception (Menozzi, 1924) to be 'closely related to *Calyptomyrmex* Em., and especially to the subgenus *Dicroaspis* Em.', and illustrated by three misleading sketches, sinks into the synonymy of *Dicroaspis.* On examination the type-species of *Geognomicus, G. wheeleri,* proved to be a straight synonym of the type-species of *Dicroaspis.*

In the Ethiopian zoogeographical region all the species of these genera nest in the ground, either directly into the soil or in rotten wood embedded in the topsoil, or under stones. The majority of species also forage and spend their entire lives in the leaf-litter but one or two species of *Meranoplus* may ascend trees or low shrubs, though none of the African species are as strongly arboreal as some of their congeners in the Indo-Australian region.

Historically the three genera *Dicroaspis, Calyptomyrmex* and *Meranoplus* were included in a single tribe, the Meranoplini, recently dissolved by Kugler (1978). This tribe was erected by Emery (1914) to include these genera along with *Mayriella* Forel, *Promeranoplus* Emery and *Prodicroaspis* Emery. The same genera constituted the tribe at the formulation of the classifications of Wheeler (1922) and Emery (1922), and by the time of the latest synopsis of the tribe by Wheeler (1935) the genera *Willowsiella* Wheeler, *Romblonella* Wheeler and *Geognomicus* (now a synonym of *Dicroaspis*) had also been added to the list. The final addition to the Meranoplini was *Ankylomyrma* Bolton, made by myself (Bolton, 1973) for reasons which I now consider to be insufficient and wrong. *Ankylomyrma* should be excluded from consideration with any of the above genera, its affinities do not lie in the direction of any of them.

Despite the removal of the anomalous *Ankylomyrma* the Meranoplini still represents an artificial assemblage of genera which in reality should not all be grouped together. The question of why they were grouped together in the first place is perhaps answered by a consideration of *Meranoplus* itself and the aberrant characters that it shows, such as deep scrobes, short alitrunk with large promesonotum, and short to absent propodeal dorsum. It happens that these characters are also present to some extent in *Calyptomyrmex* although, except for the deep scrobes, by no means as spectacularly. These superficial likenesses were considered sufficient to link the two genera. After this association was made the concept of a tribe Meranoplini was so weighted that other genera merely fell in when they showed either vaguely *Calyptomyrmex*-like or *Meranoplus*-like characters. My opinion now is that the classical Meranoplini contained two groups of genera from basically different stocks, which show fundamental differences in their clypeal structure and the construction of the petiole, as well as the differences in sting structure pointed out by Kugler (1978).

In *Meranoplus, Romblonella* and *Willowsiella* the petiole is sessile. There is no elongate anterior peduncle separating the anterior face of the node from its articulation with the alitrunk, merely a very short connecting section which is just long enough to allow the petiole to articulate in vertical plane. On the other hand, in *Calyptomyrmex* and all the other genera mentioned above the petiole has a long peduncle in front of the node so that the anterior face of the node is separated from the portion which articulates with the alitrunk by a conspicuous, more or less horizontal, bar.

The posterior portion of the clypeus in *Meranoplus, Romblonella* and *Willowsiella* is broad and broadly arched between the widely separated frontal lobes. The antennal insertions are widely separated and the frontal lobes above them are narrow. In *Calyptomyrmex* and the other genera (*Mayriella, Promeranoplus, Prodicroaspis, Dicroaspis*), the posterior portion of the clypeus is narrow and deeply inserted between the closely approximated frontal lobes. The antennal insertions are relatively close together and the frontal lobes tend to be broad. This implies that the method of formation of the upper scrobe margin may be basically different in *Meranoplus* and *Calyptomyrmex*. Members of the former needed only to fuse the laterally expanded frontal carinae to the narrow frontal lobes to create a uniform flange above the scrobe; no marked expansion of the frontal lobes was necessary to protect the base of the scape. However, in *Calyptomyrmex*, because the clypeus is so narrow posteriorly and the antennal insertions so close together, a strong expansion of the frontal lobes was necessary so that their outer margins would be roughly aligned with those of the frontal carinae and thus form a uniform flange above the scrobe without leaving much of the base of the scape unprotected when it was folded into the scrobe.

In summary then, the modifications discussed above indicate that genera from two fundamentally different stocks were originally included under the name Meranoplini, and I am in agreement with Kugler (1978; 1979) that the tribe is best dissolved. Of the former members the genera *Meranoplus, Romblonella* and *Willowsiella* are characterized by having a sessile petiole node and a clypeus which is broad and broadly arched posteriorly, but despite these similarities I am not convinced that the three genera are truly closely related. On the strength of the sting structure Kugler (1978) places *Meranoplus* in the peripheral genera of the *Pheidole*-group, but this list of peripherals also includes such disparate forms as *Crematogaster* Lund, *Myrmicaria* Saunders and *Lachnomyrmex* Wheeler, so I am suspicious of the grouping.

As regards *Romblonella* and *Willowsiella*, both show a triangular prominence on each side of the petiole near the base of the node, such as is commonly seen in leptothoracines, but whether there is any sort of relationship remains to be seen, although there are similarities between *Romblonella* and some tropical species of *Leptothorax*.

The second group of genera, including *Calyptomyrmex, Mayriella, Dicroaspis, Prodicroaspis* and *Promeranoplus*, have the petiole pedunculate and the posterior portion of the clypeus narrow and deeply inserted between the frontal lobes. My present opinion is that members of this group are genuinely related as, besides the characters just mentioned, they have a characteristically shaped alitrunk where the promesonotum is fused (and commonly somewhat swollen), followed by a low propodeum which often has a strongly sloping dorsal surface. On present evidence I consider that *Calyptomyrmex* and its allies are related to the *Lordomyrma*-group of genera.

Kugler's (1978; 1979) studies of the myrmicine sting show partial agreement since he groups *Lordomyrma* Emery, *Promeranoplus* and *Prodicroaspis* together (as the *Promeranoplus*-group), but he puts *Calyptomyrmex* in the peripheral genera of the *Solenopsis*-group. It is possible that *Solenopsis* Westwood and allies, *Calyptomyrmex* and allies, and *Lordomyrma* may be more closely related than was previously thought, but more work will be necessary on many of the genera involved before any real conclusions can be reached. It is, however, interesting to note that Kugler (1979: 122) has placed *Calyptomyrmex* and 'the primitive species of the *Solenopsis*- and *Promeranoplus*-groups' together in the second section of genera with a grade 2 sting apparatus.

Measurements and indices

Total Length (TL). The total outstretched length of the individual, from mandibular apex to gastral apex.

Head Length (HL). The length of the head proper, excluding the mandibles; measured in *Meranoplus* in a straight line from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin, in full-face view. In *Calyptomyrmex* and *Dicroaspis* the head length is measured from the base of the clypeal fork to the mid-point of the occipital margin, in a straight line in full-face (after Urbani, 1975).

Head Width (HW). The maximum width of the head behind the eyes, measured in full-face view.

Cephalic Index (CI). $\frac{HW \times 100}{HL}$

Scape Length (SL). The straight-line length of the antennal scape, excluding the basal constriction or neck close to the articulating condylar bulb.

Scape Index (SI). $\frac{SL \times 100}{HW}$

Pronotal Width (PW). In *Calyptomyrmex* and *Dicroaspis* the maximum width of the pronotum in dorsal view. In *Meranoplus* the width of the pronotum behind the pronotal teeth, in dorsal view.

Alitrunk Length (AL). In *Calyptomyrmex* and *Dicroaspis* the diagonal length of the alitrunk in lateral view from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobes. In *Meranoplus* the same measurement but commencing at the pronotal tooth.

All measurements are expressed in millimetres.

Abbreviations of museums

AMNH, New York	American Museum of Natural History, New York, U.S.A.
BMNH	British Museum (Natural History), London, U.K.
IE, Bologna	Instituto di Entomologia del'Università, Bologna, Italy.
MCSN, Genoa	Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy
MCZ, Cambridge	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHN, Geneva	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN, Paris	Muséum National d'Histoire Naturelle, Paris, France
MRAC, Tervuren	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NM, Basle	Naturhistorisches Museum, Basle, Switzerland
NM, Bulawayo	National Museum, Bulawayo, Zimbabwe
NM, Vienna	Naturhistorisches Museum, Vienna, Austria

MERANOPLUS F. Smith

(Figs 1–25)

Meranoplus F. Smith, 1853: 224. Type-species: *Cryptocerus bicolor* Guérin-Méneville, 1844: 425, by subsequent designation of Bingham, 1903: 166.

[*Cryptocephalus* Lowne, 1865: 336. Incorrect subsequent spelling of *Cryptocerus* Latreille in the combination *Cryptocephalus pubescens* Smith (= *Meranoplus pubescens* (Smith)).]

DIAGNOSIS OF WORKER. Myrmicine ants in which the mandibles have a short masticatory margin, with 4–5 teeth (either 5 teeth, 4 teeth plus offset basal denticle, or 4 teeth only). Palp formula 5, 3 (all African species plus 14 extralimital species dissected; in very small species the basal maxillary palpomere may be short so that the PF appears to be 4, 3). Clypeus large, the median portion shield-like, usually carinate at each side or with the dorsum and sides separated by an angle. Posterior section of median portion of clypeus broad and broadly arched posteriorly, not narrowly inserted between the frontal lobes. Antennal scrobes present, deep and usually long, bounded above by the widely separated frontal carinae and below by a sharp ridge which runs to the eye. Scapes thicker in apical than in basal halves. Antennae with 9 segments, the apical 3 flagellar segments forming a club. Eyes large, situated behind midlength of head, sometimes close to the occipital corners; eyes located below the antennal scrobes and usually close to their apices. (The eyes more or less central on the head in a few Australian species, in which the scrobes are also reduced.) Ventral surface of head with a longitudinal ridge or carina on each side. Pronotum and mesonotum fused into a plate or shield which is usually extended posteriorly and laterally so that the sides of the alitrunk and generally also the propodeum are invisible in dorsal view (not in *spininodis*-group). Lateral and/or posterior margins of promesonotal shield commonly armed with spines, lobes, foliacious processes or other outgrowths, the body of the promesonotal shield sometimes with cuticular thin-spots or fenestrae. Petiole sessile, without an anterior peduncle, the node usually cuneate in profile, broadest basally and narrowing above; high-nodiform in some extralimital species.

Meranoplus is a relatively small compact genus of ants found throughout the Old World tropics and subtropics but with the greatest number of species in Australia. Discounting synonyms and infraspecific forms some 47 species have been described to the present. Of these, only eight occur in sub-Saharan Africa with varying degrees of success. The species *glaber, spininodis, sthenus* and *peringueyi* are known only from the countries of the southern portion of Africa, namely Zimbabwe, Botswana, South Africa and Lesotho. Two other species, *nanus* and *clypeatus,* are rather more widely distributed but are not known from the afore-mentioned territories, being of more northerly distribution in the continent. The last two species, *inermis* and *magrettii,* are extremely widely distributed in Africa, both being known from Sudan to South Africa and from West to East Africa. The difference in their distribution is that *inermis* is primarily a species of forests whilst *magrettii* is found mainly in savannah.

All the African species nest directly into the ground, either in the open where the nest entrance may form a small crater, or at the base of plants where the nest may be built amongst the roots.

Most of the species of Africa show marked variation in size between different nests of the same species, and commonly between individuals from a single nest there are noticeable size-differences. In many cases the differences in size are linked to changes in other characters such as intensity and density of sculpture, presence or absence of sutures, length of mesonotal spines etc. Intrinsically variable characters such as this were responsible for the creation of most of the infraspecific taxa which are now synonymized. The status of the various African forms is now as shown in the following list.

Synonymic list of species

***spininodis*-group**
- ***glaber*** Arnold **stat. n.**
- ***spininodis*** Arnold
- ***sthenus*** **sp. n.**

***nanus*-group**
- ***clypeatus*** Bernard
- ***inermis*** Emery
    - *nanus* subsp. *nanior* Forel **syn. n.**
    - *nanus* var. *kiboshana* Forel **syn. n.**
    - *nanus* subsp. *soriculus* Wheeler **syn. n.**
    - *nanus* subsp. *similis* Karavaiev (homonym)
    - *nanus* subsp. *affinis* Urbani **syn. n.**
- ***nanus*** André

***magrettii*-group**
- ***magrettii*** André
    - *simoni* Emery **syn. n.**
    - *simoni* subsp. *nitidiventris* Mayr **syn. n.**
    - *simoni* subsp. *suturalis* Forel **syn. n.**
    - *bondroiti* Santschi **syn. n.**
    - *simoni* var. *springvalensis* Arnold **syn. n.**
    - *simoni* var. *diversipilosus* Santschi **syn. n.**
- ***peringueyi*** Emery
    - *excisus* Arnold **syn. n.**

Key to species (workers)

1 Dorsum of petiole armed with a pair of spines or teeth (Figs 1–3). Promesonotal shield posteriorly not overhanging the propodeum, the latter visible in dorsal view and forming a part of the dorsal alitrunk (Figs 1–3, 9–11) 2

– Dorsum of petiole unarmed, without spines or teeth. Promesonotal shield posteriorly overhanging the propodeum, the latter not visible in dorsal view and not forming a part of the dorsal alitrunk (Figs 4–7, 12–25) 4

2 Erect to suberect stout hairs absent from dorsal (outer) surface of hind tibiae, only fine decumbent to appressed pubescence present. Dorsal surfaces of head, alitrunk and gaster with short appressed hairs, without elongate erect or suberect pilosity (Fig. 2). (Zimbabwe, Botswana) . . . . **glaber** (p. 49)

– Erect to suberect stout hairs present on dorsal (outer) surface of hind tibiae. Dorsal surfaces of head, alitrunk and gaster with conspicuous elongate pilosity which may be very dense and which is erect or suberect at least in part (Figs 1, 3) 3

3 Postpetiole in profile low and broad, nodiform, the posterodorsal angle prominent and overhanging the shallowly concave posterior face (Fig. 3). Dorsum of postpetiole densely clothed in fine soft curved hairs. Spines on petiole dorsum short. (Zimbabwe, Botswana) **spininodis** (p. 50)

– Postpetiole in profile high and narrow, columnar, the posterodorsal angle not prominent, not overhanging the posterior face (Fig. 1). Dorsum of postpetiole with a few long stout hairs and some short, fine pubescence. Spines on petiole dorsum long. (Zimbabwe) . . **sthenus** (p. 50)

4 Postpetiole in profile squamiform or very strongly anteroposteriorly compressed, without a long dorsal surface (Figs 4, 5). Propodeal spines absent or short, not projecting posteriorly beyond the mesonotal margin in dorsal view 5

– Postpetiole in profile broad and nodiform, with a long dorsal surface which is flat to convex (Figs 6, 7). Propodeal spines projecting posteriorly beyond the mesonotal margin in dorsal view 7

5 Propodeum armed with a pair of short spines (Fig. 4) 6

– Propodeum without spines (Fig. 5). (Sudan, Kenya, Tanzania, Zimbabwe, South Africa, South West Africa, Angola, Zaire, Nigeria, Ghana) . . . . **inermis** (p. 52)

6 Posterior margin of mesonotum with 4–6 opaque cuticular projections, the spaces between the projections with translucent thin cuticular lamellae (Fig. 12). Postpetiole dorsum a transverse crest without rugose sculpture. (Gabon, Zaire, Tanzania) . . . . . . **nanus** (p. 53)

– Posterior margin of mesonotum with a broad transverse shelf-like lamella which may project into 2–4 flat triangular teeth, the lamella usually concave and thinner medially (Figs 13–15). Postpetiole dorsum narrow but flattened, with rugose sculpture. (Guinea, Zaire) **clypeatus** (p. 52)

7 Mandibles armed with 5 teeth. Anterior clypeal apron rounded and generally shallowly convex, without a prominence or denticle on each side of the median portion. (South Africa, Lesotho) **peringueyi** (p. 56)

– Mandibles armed with 4 teeth. Anterior clypeal apron more or less flat to concave between a prominence or denticle on each side of the median portion (Fig. 8). (Ghana, Sudan, Uganda, Kenya, Tanzania, Zimbabwe, Botswana, South Africa) . . . . . . **magrettii** (p. 55)

The species-groups

The eight species of *Meranoplus* present in the Ethiopian zoogeographical region divide easily into three approximately equal-sized groups of related forms. The members of the first group, which includes *glaber, spininodis* and *sthenus* (Figs 1–3, 9–11), are characterized by possessing a pair of spines or teeth upon the petiolar dorsum. Besides this the promesonotal shield is not as well developed as in the remaining groups and does not completely overhang the propodeum, so that the latter constitutes a part of the dorsal alitrunk and is visible in dorsal view.

In the two remaining groups the petiole is unarmed and the promesonotal shield much more strongly developed, completely overhanging the near-vertical propodeum so that the latter is not visible in dorsal view and does not constitute a part of the dorsal alitrunk.

Of these two groups the species related to *nanus* (*clypeatus* and *inermis*, Figs 4, 5, 12–19) have the postpetiole squamiform whilst the species of the *magrettii*-group (*magrettii* and *peringueyi*, Figs 6–8, 20–25) have the postpetiole strongly nodiform. As well as this difference in postpetiolar structure *nanus* and its allies either lack propodeal spines (*inermis*) or have them quite short, in dorsal view not projecting beyond the mesonotal margin, whereas in *magrettii*-group the propodeal spines are long and conspicuous.

The *spininodis*-group

(Figs 1–3, 9–11)

Mandibles with five teeth, consisting of four large distinct teeth and a small offset basal denticle. With the alitrunk in dorsal view the propodeum constituting a part of the dorsum, visible as a narrow transverse strip behind the promesonotal shield and bearing a pair of massive spines. Anterior pronotal corners dentate, posterior mesonotal corners each with a short triangular spine which is much less massive than the spines borne on the propodeum. Dorsal surface of petiole narrow and armed with a pair of teeth or spines. Postpetiole in profile columnar or nodiform, not squamiform.

These diagnostic characters link three small species known from Zimbabwe and Botswana and easily separate them from all other species of the genus in this region. In fact, the bispinose petiole does not seem to occur in any other *Meranoplus* species, making the *spininodis*-group unique to southern Africa.

Of the three *glaber* is separated by its lack of erect/suberect stout hairs on the body and the lack of such hairs on the tibiae. In both *sthenus* and *spininodis* such hairs are numerous and conspicuous. These last two species are differentiated chiefly on the shape of the postpetiole and the length of the petiolar spines. In *spininodis* the petiolar spines are short and the postpetiole has a projecting posterodorsal angle which overhangs the concave posterior face of the postpetiole (Fig. 3). In *sthenus* on the other hand the petiolar spines are long and the postpetiole columnar, lacking a projecting posterodorsal angle and with a vertical posterior face (Fig. 1).

Meranoplus glaber Arnold **stat. n.**

(Figs 2, 10)

Meranoplus spininodis var. *glaber* Arnold, 1926: 285, fig. 82. Syntype workers, ZIMBABWE: Bulawayo, Hillside, 13.v.1917; Sawmills, 30.i.1918 and 1.ii.1918 (*G. Arnold*) (BMNH; NM, Bulawayo) [examined].

WORKER. TL 2·3–3·1, HL 0·60–0·72, HW 0·58–0·72, CI 97–103, SL 0·36–0·44, SI 60–64, PW 0·54–0·72, AL 0·50–0·80 (14 measured).

Mandibles striate, the masticatory margin armed with four teeth plus a small, offset basal denticle. Median portion of clypeus with a narrow translucent apron anteriorly which projects over the bases of the mandibles and conceals the basal tooth and denticle when the mandibles are closed. A longitudinal carina present on each side of the median portion of the clypeus, running forward to the anterior apron and separating the more or less flat dorsum from the sides. Eyes large and conspicuous, maximum diameter 0·61–0·21 (about 0·28–0·30 × HW) and with 10–12 ommatidia in the longest row. Promesonotal shield strongly marginate laterally, the pronotal portion slightly broader than the mesonotal in dorsal view. Anterior pronotal angles projecting as short, broad triangular teeth, posterior mesonotal angles projecting as stout teeth or short triangular spines, which are usually longer than the pronotal teeth. Margins of promesonotal shield without fenestrae or thin-spots, without cuticular outgrowths other than the teeth described above. Propodeum visible in dorsal view as a thin transverse strip behind the promesonotal shield and bearing a pair of long, stout, usually slightly incurved spines. Petiole narrow cuneate, thicker at the base and tapering above in profile, the dorsal surface armed with a pair of teeth which are usually distinctly shorter than the distance separating their bases, rarely otherwise. Ventral process of petiole a very thin translucent lamella which runs forward from the posteroventral bulge almost to the articulation. Postpetiole thick in dorsal view, broader than long, not squamate. In profile postpetiole roughly columnar, the anterior face slightly convex, the posterior face slightly concave and with rounded angles. Subpostpetiolar process elongate-triangular in profile. Dorsum of head faintly longitudinally rugulose, the occipital region and the promesonotal shield delicately reticulate-rugulose. First gastral tergite finely superficially reticulate-punctulate or shagreened basally, this sculpture fading out or diminishing apically on the sclerite. Erect or suberect hairs absent from dorsal surfaces of head and body, all hairs short and decumbent to appressed. Stout standing hairs absent from dorsal (outer) surfaces of middle and hind tibiae. Colour either uniform pale yellow or with the gaster darker in shade than the head and alitrunk.

This small species, originally described as a variety of *spininodis*, is characterized within this group by its lack of standing hairs on the head and body and lack of projecting tibial hairs on the legs. Such hairs are present and conspicuous in both *sthenus* and *spininodis*. Besides the pilosity *glaber* differs from *spininodis* in the construction of the postpetiole, which in the latter is strongly nodiform in profile with a projecting posterodorsal angle.

MATERIAL EXAMINED

Zimbabwe: Sawmills (*G. Arnold*). **Botswana**: Maxwee (*A. Russell-Smith*).

Meranoplus spininodis Arnold

(Figs 3, 11)

Meranoplus spininodis Arnold, 1917: 366. Holotype and paratype workers, ZIMBABWE: Bulawayo, Hillside, 9.vi.1916 (*G. Arnold*) (BMNH) [examined].

WORKER. TL 2·8–3·6, HL 0·66–0·76, HW 0·66–0·76, CI 97–103, SL 0·40–0·50, SI 60–65, PW 0·66–0·74, AL 0·68–0·80 (16 measured).

Mandibles striate, equipped with four teeth plus a small offset basal denticle, the latter concealed by the clypeus when the mandibles are closed. Anterior clypeal margin with a narrow translucent apron, the median portion bounded on each side by a longitudinal carina which runs forward to the apron. Maximum diameter of eye 0·18–0·21 (0·26–0·29 × HW), with 11–13 ommatidia in the longest row. Promesonotal shield strongly marginate laterally, the pronotal portion slightly wider than the mesonotal. Anterior pronotal angles with a pair of teeth, the posterior mesonotal angles armed with a pair of short stout triangular spines. Margins of promesonotal shield without fenestrae or thin-spots, without cuticular outgrowths other than those described above. Propodeum visible in dorsal view as a thin transverse strip behind the promesonotal shield, and bearing a pair of long, stout, very conspicuous spines. Petiole cuneate in profile, tapering from base to apex and armed dorsally with a pair of teeth or short spines which are usually distinctly shorter than the distance separating their bases. Subpetiolar process an anteriorly situated translucent lamella which is commonly produced into a downcurved lobe anteroventrally. Postpetiole nodiform, its ventral process triangular. In profile the posterodorsal angle of the postpetiole produced so that it overhangs the shallowly concave posterior face of the node. Sculpture on head and promesonotal shield of fine rugulae, usually with reticulation on the occiput and at least on the pronotal portion of the shield. Dorsum of postpetiole finely rugulose. First gastral tergite densely reticulate-punctate, at least at base; sometimes this sculpture extending over the entire sclerite but more usually with it fading out posteriorly. All dorsal surfaces of head and body thickly clothed with fine, dense, elongate simple hairs, most of which are curved and some or all of which are erect or suberect. Dorsal (outer) surface of middle and hind tibiae with outstanding hairs. Colour varying from mid-brown with darker gaster through to uniform dark brown.

Easily recognized within the group by its abundance of long curved hairs and thick postpetiole with overhanging posterior angle. It is distinguished from *glaber* by the lack of standing pilosity and projecting tibial hairs in that species, and from *sthenus* by the sparse erect hairs of that species and its differently constructed postpetiole, as described under the description of that species.

MATERIAL EXAMINED

Zimbabwe: Bulawayo (*G. Arnold*); Sawmills (*G. Arnold*). **Botswana:** between Kastwe and Damana Pan (*H. Lang*).

Meranoplus sthenus **sp. n.**

(Figs 1, 9)

HOLOTYPE WORKER. TL 3·1, HL 0·76, HW 0·74, CI 97, SL 0·48, SI 65, PW 0·74, AL 0·78.

Mandibles striate, armed with four teeth and a small offset basal denticle, the latter concealed by the clypeus when the mandibles are closed. Median portion of clypeus with a narrow translucent apron anteriorly and bounded on each side by a low longitudinal carina which runs forward to the apron. Maximum diameter of eye 0·20 (0·27 × HW), with 11–12 ommatidia in the longest row. Promesonotal shield sharply marginate laterally, the pronotal portion slightly broader than the mesonotal. Anterior pronotal angles with a pair of triangular teeth, the posterior mesonotal angles with broad triangular teeth or short spines. Apart from these teeth the promesonotal shield unadorned, without fenestrae or thin-spots and without cuticular outgrowths. Propodeum visible in dorsal view as a transverse strip behind the promesonotal shield, bearing a pair of long, stout spines. Petiole in profile cuneate, tapering from base to apex and with a translucent lamellate ventral process. Dorsum of petiole armed with a pair of spines which are longer than the distance separating their bases. Postpetiole in profile columnar, with roughly parallel anterior and posterior faces and rounded angles. Subpostpetiolar process triangular in profile. Sculpture on head and promesonotal shield of fine rugulae, with a reticulum on the occipital surface and the pronotum. Base of first gastral tergite finely and superficially punctulate, this sculpture weakening posteriorly. All dorsal surfaces of head and body with sparse erect to suberect long strong hairs but lacking dense fine soft long pilosity. Middle and hind tibiae with outstanding hairs. Colour yellowish brown with the gaster slightly darker.

PARATYPE WORKERS. TL 2·8–3·2, HL 0·70–0·78, HW 0·68–0·74, CI 94–97, SL 0·46–0·52, SI 65–68, PW 0·68–0·74, AL 0·66–0·82 (10 measured).

Maximum diameter of eye 0·20–0·22 (0·27–0·29 × HW), with 11–13 ommatidia in the longest row. Paratypes as holotype but in some the gaster distinctly darker than the remainder and the petiolar spines slightly shorter. The base of the first gastral tergite is usually as holotype but in a few the sculpture is almost effaced.

Holotype worker, **Zimbabwe:** Sawmills, 1.ii.1918 (*G. Arnold*) (BMNH).

Paratypes. **Zimbabwe:** 13 workers and 1 female with same data as holotype; 2 workers, Sawmills 30.i.1918 (*G. Arnold*); 8 workers, Victoria Falls, 22.ii.1953 (*G. Arnold*) (BMNH; NM, Bulawayo; MCZ, Cambridge; MRAC, Tervuren).

The final species of the *spininodis*-group, *sthenus* was first collected by Arnold together with a few workers of *glaber*, but he considered them to be expressions of a single species as he thought that they were all from a single nest. However, as extra collections of both forms were made later and as queens of both are now known which show the same separational characters as the workers, it is apparent that the original series was mixed or that some specimens were inadvertantly mislabelled.

M. sthenus separates easily from *glaber* as the latter lacks long erect to suberect hairs on the body and lacks outstanding tibial hairs. It is separable from *spininodis* on the following characters.

spininodis	*sthenus*
Postpetiole nodiform, the posterodorsal angle prominent and overhanging the posterior face.	Postpetiole columnar, the posterodorsal angle not prominent, not overhanging the posterior face.
Petiolar spines short, usually distinctly shorter than the distance separating their bases.	Petiolar spines long, usually distinctly longer than the distance separating their bases.
Alitrunk and gaster with a dense pelt of long soft curved hairs.	Alitrunk and gaster without a dense pelt of long soft curved hairs.

The *nanus*-group

(Figs 4, 5, 12–19)

Mandibles with four teeth. With the alitrunk in dorsal view the propodeum concealed, not constituting a part of the dorsum. Petiole cuneate in profile, its dorsal surface unarmed, without spines or teeth. Postpetiole squamate or at least very strongly antero-posteriorly compressed. Promesonotal shield short and broad. Propodeal spines short or absent.

Of the three African species constituting this group two (*clypeatus* and *nanus*) are much less common than the third (*inermis*) which is very widely distributed in woodland and forest throughout the continent. Lacking propodeal spines, *inermis* is quickly separated from the other members of this group and from all other African species, as propodeal spines are otherwise universally present, even if small. *M. clypeatus*, known from Guinea and Zaire, has the postpetiole somewhat thicker than in the similarly distributed *nanus* (Gabon, Zaire, Tanzania) and the form of the mesonotal posterior margin differs between the two, as discussed below.

Meranoplus clypeatus Bernard

(Figs 13–15)

Meranoplus clypeatus Bernard, 1952: 244, fig. 13C. Syntype workers, female, GUINEA: Mt Nimba, station F, prairie, 1400 m (*Lamotte*); and prairie, 1550 m (*Lamotte*) (MNHN, Paris) [examined].

WORKER. TL 2·8–3·8, HL 0·76–0·88, HW 0·74–0·84, CI 95–100, SL 0·58–0·66, SI 74–79, PW 0·78–0·90, AL 0·74–0·90 (6 measured).

Mandibles striate, armed with four teeth. Anterior margin of median portion of clypeus shallowly concave and with a narrow translucent apron. Sides of median portion of clypeus with a weak longitudinal carina, the surface between the carinae weakly concave in the anterior half. Maximum diameter of eye 0·19–0·20 (0·24–0·26 × HW), with 10–12 ommatidia in the longest row. Promesonotal shield in dorsal view conspicuously broader than long, strongly marginate and expanded laterally and posteriorly and overhanging the propodeum and sides of the alitrunk which are not visible. Anterior pronotal corners dentate. Shield at junction of pronotum and mesonotum with a thin-spot on each side which may be a roughly circular fenestra set in from the margin or which may be extended to the lateral margin. Promesonotal suture usually absent but sometimes a faint line visible traversing the dorsum between the thin-spots. Ouline shape of posterior mesonotal margin variable (Figs 13–15) but without strong cuticular prominences separated by conspicuous thin-spots. A posteromedian thin-spot occurs in some specimens but usually the posterior mesonotal margin is a broad shelf-like lamella which projects into 2–4 flat, roughly triangular teeth. Propodeum in profile nearly vertical, armed at about its mid-depth with a pair of short spines. Petiole in profile cuneate, broadest basally and narrowing above; in anterior view the dorsal face rounded. Postpetiole in profile strongly anteroposteriorly compressed but not as obviously squamiform as in other members of this group. Dorsum of postpetiole narrow and sculptured, not a transverse crest. Head predominantly finely longitudinally rugose, commonly with scattered cross-meshes and usually with a weak reticulum occipitally. Promesonotal shield finely and irregularly reticulate-rugulose, the intensity of sculpture variable, usually stronger in larger specimens. Narrow postpetiole dorsum rugulose or reticulate-rugulose. First gastral tergite finely shagreened to virtually smooth. All dorsal surfaces of head and body, legs and scapes densely clothed with a pelt of long soft fine hairs. Colour uniform medium to dark brown.

Within the *nanus*-group *clypeatus* is distinguished by its somewhat thicker, dorsally sculptured postpetiole. In *nanus* and *inermis* the postpetiole is squamate with the dorsal surface an unsculptured transverse crest. Apart from this *inermis* lacks propodeal spines (present in *clypeatus*) and the posterior mesonotal margin of *nanus* consists of 4–6 thick cuticular projections separated by extensive translucent thin-spots.

MATERIAL EXAMINED

Zaire: Kurukwata, nr Aba (*Myers*).

Meranoplus inermis Emery

(Figs 5, 16–19)

Meranoplus inermis Emery, 1895: 41, pl. 2, fig. 24. Syntype workers, SOUTH AFRICA: Makapan (*E. Simon*) (MCSN, Genoa) [examined].

Meranoplus nanus subsp. *nanior* Forel, 1907: 12. Syntype workers, KENYA: Mto-ya-Kifaru (*Katona*) (MHN, Geneva) [examined]. **Syn. n.**

Meranoplus nanus var. *kiboshana* Forel, 1907: 12. Syntype workers, KENYA: Kibosho (*Katona*) (MHN, Geneva) [examined]. **Syn. n.**

Meranoplus nanus subsp. *soriculus* Wheeler, 1922: 184, fig. 45. Syntype workers, females, males, ZAIRE: Avakubi (*H. O. Lang*) (MCZ, Cambridge; BMNH; MRAC, Tervuren) [examined]. **Syn. n.**

Meranoplus nanus subsp. *similis* Karavaiev, 1931: 44, fig. 3. Holotype worker, KENYA: Mabira (*Dogiel & Sokolow*) (location of type not known). [Junior primary homonyn of *Meranoplus similis* Viehmeyer, 1922: 208.]

Meranoplus nanus subsp. *affinis* Urbani, 1971: 361. [Replacement name for *Meranoplus nanus* subsp. *similis* Karavaiev.] **Syn. n.**

WORKER. TL 2·7–4·0., HL 0·68–0·90, HW 0·64–0·84, CI 93–98, SL 0·42–0·64, SI 65–75, PW 0·66–0·90, AL 0·58–0·88 (20 measured).

Mandibles striate, armed with four teeth. Anterior clypeal margin with a narrow translucent apron and with a longitudinal carina on each side of the median portion which runs forwards to the apron. Anterior half of clypeus usually shallowly concave between the carinae. Maximum diameter of eye 0·16–0·20. (0·23–0·25 × HW), with 9–12 ommatidia in the longest row. Promesonotal shield in dorsal view conspicuously broader than long, marginate and strongly expanded laterally and posteriorly, concealing the sides and propodeum which are not visible. Anterior pronotal corners dentate. A thin-spot or fenestra is present at each side at the junction of pronotum and mesonotum; commonly this thin-spot is approximately circular and set in from the lateral margin, but often it is elongate and reaches out to the margin. Sometimes the spot is small but it is usually conspicuous, even in the smallest specimens. Promesonotal suture vestigial or absent, at most represented only by a very weak line traversing the shield between the thin-spots. Posterior mesonotal border of variable shape, most commonly with a posterolateral broad angle followed by 2–4 flat projections on the posterior border. The inner pair of projections usually less strongly developed than the outer and with an area of thinner cuticle between them. Sometimes the projections all strong but sometimes all reduced, especially in smaller individuals, so that the margin appears broadly crenulate. Propodeum in profile nearly vertical, unarmed, without trace of teeth or spines but sometimes with a small step or convexity at about the level of the spiracle. Petiole in profile cuneate, broadest basally and tapering above; in anterior view the dorsal surface rounded. Postpetiole squamate, sometimes almost as narrow as the petiole, the dorsal surface a transverse blunt crest which is thicker than that of the petiole. Dorsum of head finely and sometimes quite densely rugulose, the rugulae predominantly longitudinal with a few cross-meshes, and finely reticulate on the occiput. In some samples, usually of smaller individuals, the cephalic sculpture very reduced with just a few faint rugulae; in others the sculpture strong and quite dense, often with numerous cross-meshes. Promesonotal shield varying from finely and densely reticulate-rugulose everywhere to almost smooth with just a few faint irregular rugulae scattered over the surface. Postpetiole dorsum unsculptured or at most with faint shagreening. First gastral tergite generally unsculptured except for hair-pits but sometimes shagreened basally. All dorsal surfaces of head and body, along with legs and scapes, with a dense pelt of long, soft fine hairs. Colour varying from mid to dark brown but often with the gaster darker in shade than the rest.

M. inermis is the only species in this group, and the only known African species, to lack propodeal spines. Apart from this difference the two other species in the group are separated from *inermis* by the thicker, dorsally sculptured postpetiole in *clypeatus*, and the differently shaped posterior mesonotal margin in *nanus* which has 4–6 opaque projections separated by very thin translucent cuticle.

The synonyms noted above, although all originally attached to *nanus*, belong in fact to *inermis*. This was due to confusion between the two species as discussed under *nanus*.

M. inermis is one of the two commonest species of *Meranoplus* in Africa (the other is *magrettii*). It is found nesting in the ground in wooded or forested areas almost throughout the continent.

MATERIAL EXAMINED

Sudan: Kadugli (*C. Sweeney*); Imatong Mts (*N. A. Weber*). **Kenya:** Magombo-Kisii (*P. v. d. Werff*); Mtito Andei (*N. A. Weber*). **Tanzania:** Bunduki, Uluguru Mts (*P. Basilewsky & N. Leleup*). **Ghana:** Kibi (*D. Leston*); Asamankese (*D. Leston*); Tafo (*H. E. Box*); Mampong (*P. Room*). **Nigeria:** Gambari (*B. Taylor*); Gambari (*B. Bolton*); Mokwa (*C. Longhurst*); Ile-Ife (*J. T. Medler*). **Zaire:** Medje (*H. O. Lang*); Haut Uele, Moto (*L. Burgeon*); Katanga, Kanzenze *N. Leleup*); Yangambi (*Raignier & van Boven*). **Angola:** Bruco (*P. Hammond*); Salazar (*P. Hammond*); Gabela (*P. Hammond*). **South West Africa:** Okahanja (*R. E. Turner*). **Zimbabwe:** Bulawayo (*G. Arnold*); Victoria Falls (*G. Arnold*).

Meranoplus nanus André

(Figs 4, 12)

Meranoplus nanus André, 1892: 55. Syntype workers, GABON (*Mocquerys*) (MNHN, Paris) [examined].

WORKER. TL 2·8–3·8, HL 0·78–0·92, HW 0·74–0·86, CI 93–95, SL 0·56–0·70, SI 75–81, PW 0·80–0·90, AL 0·70–0·86 (10 measured).

Mandibles striate, armed with four teeth. Anterior clypeal margin with a narrow translucent apron and with a longitudinal carina on each side of the median portion which runs forwards to the apron. Anterior half of clypeus usually shallowly concave between these carinae. Maximum diameter of eye 0·20–0·22

(0·24–0·27 × HW), with 10–12 ommatidia in the longest row. Promesonotal shield in dorsal view conspicuously broader than long, marginate and strongly expanded laterally and posteriorly, concealing the sides and propodeum which are not visible. Anterior pronotal corners dentate. A thin-spot or fenestra present at the junction of pronotum and mesonotum; usually this thin-spot is roughly circular and set in from the margin but sometimes it is elongate and reaches out to the margin. Promesonotal suture absent or vestigial, at most represented by a fine line or break in the sculpture which traverses the shield between the thin-spots. Posterior mesonotal border adorned with 4–6 flattened opaque cuticular prominences separated by very thin translucent lamellae; shape and size of the projections variable but generally as in Fig. 12. Propodeum in profile nearly vertical, armed at about the mid-depth with a pair of short, stout spines. Petiole in profile cuneate, broadest basally and tapering above; in anterior view the dorsal surface rounded. Postpetiole squamate, the dorsal surface a transverse blunt crest which is, however, thicker than that of the petiole. Dorsum of head finely rugulose and usually quite densely so. Sometimes entire dorsum reticulate-rugulose but usually only occiput thus, the remainder being predominantly longitudinally sculptured with scattered cross-meshes. Intensity of sculpture on both head and alitrunk variable, generally sharply defined but fainter in some. Promesonotal shield finely, and usually densely, irregularly reticulate-rugulose. Dorsum of postpetiole unsculptured or at most with fine punctulae, never rugulose. First gastral tergite usually finely shagreened, at least basally, but this sculpture sometimes reduced so that the sclerite is almost smooth. All dorsal surfaces of head and body, along with legs and scapes, with a dense pelt of long soft fine hairs. Colour varying from mid to dark brown, but usually the gaster darker in shade than the head and alitrunk.

Of the two species closely related to *nanus, inermis* is identified by its lack of propodeal spines, and *clypeatus* by its strongly sculptured postpetiole dorsum and differently constructed posterior mesonotal margin, as noted in the description of that species.

For some reason there seems to have been a great deal of confusion over the identities of *nanus* and *inermis,* although the important differences between the two were stated quite plainly in the original description of the latter. André (1892) noted that the propodeum of *nanus* was armed with spines and Emery (1895), in his description of *inermis,* pointed out that the main difference between *nanus* and *inermis* was that propodeal spines were absent in the latter. Despite this a number of infraspecific forms without spines were attached to *nanus* and the original descriptions apparently ignored. The culmination of this came with Arnold (1917: 364) who, in his key to *Meranoplus,* runs out both *nanus* and *inermis* under 'epinotum (=propodeum) unarmed', whilst on the opposite page he reproduces the original descriptions of the two which flatly contradict the statement in the key.

Examination of the types and original descriptions of the infraspecific forms attached to *nanus* has shown them all to be synonyms of the much more common *inermis*.

MATERIAL EXAMINED

Zaire: Haut Uele, Abimva (*L. Burgeon*); Katanga, Kanzenze (*N. Leleup*). **Tanzania:** Zanzibar (*M. J. Way*).

The *magrettii*-group

(Figs 6–8, 20–25)

Mandibles with 4 or 5 teeth. With the alitrunk in dorsal view the propodeum concealed, not constituting a part of the dorsum. Petiole cuneate in profile, its dorsal surface unarmed, without spines or teeth. Postpetiole broad and nodiform. Promesonotal shield not particularly short and broad. Propodeal spines present.

Of the two species in this group *magrettii* is one of the most common and widely distributed species in the region, being found almost everywhere in savannah, grassland and dry woodland. The second species, *peringueyi,* is apparently restricted to South Africa.

The two species are easily distinguished as *peringueyi* has 5 teeth on each mandible and lacks clypeal armament, whilst *magrettii* has only 4 teeth and has the anterior clypeal margin with a denticle or prominence on each side of the median portion.

Meranoplus magrettii André

(Figs 7, 8, 23–25)

Meranoplus magrettii André, 1884: 543. Syntype worker, SUDAN: Sauakin [=Suakin] (*Magretti*) (MNHN, Paris) [examined]. [Second syntype worker reported by Emery (1886: 366) to be in MCSN, Genoa; not seen.]

Meranoplus simoni Emery, 1895: 41, pl. 2, fig. 23. Holotype worker, SOUTH AFRICA: Vrijburg (*E. Simon*) (MCSN, Genoa) [examined]. **Syn. n.**

Meranoplus simoni subsp. *nitidiventris* Mayr, 1901: 26. Syntype workers, SOUTH AFRICA: Orange Free State, Bothaville (*H. Brauns*) (NM, Vienna). **Syn. n.**

Meranoplus simoni subsp. *suturalis* Forel, 1910*a*: 424. Syntype workers, SOUTH AFRICA: Natal (*Haviland*) (MHN, Geneva) [examined]. **Syn. n.**

Meranoplus bondroiti Santschi, 1915: 254, fig. 4. Holotype worker, EAST AFRICA: 'région des grands lacs, Uzaga' (*Gérard*) (NM, Basle) [examined]. **Syn. n.**

Meranoplus simoni var. *springvalensis* Arnold, 1917: 372. Holotype and paratype workers, ZIMBABWE: Springvale, 12.xi.1911 (*G. Arnold*) (BMNH; NM, Bulawayo) [examined]. **Syn. n.**

Meranoplus simoni var. *diversipilosus* Santschi, 1932: 388. Syntype workers, ZIMBABWE: Sawmills, 12.vii.1920 (*G. Arnold*) (NM, Basle; NM, Bulawayo) [examined]. **Syn. n.**

WORKER. TL 2·8–4·3, HL 0·72–1·00, HW 0·64–0·94, CI 90–98, SL 0·48–0·72, SI 72–78, PW 0·58–0·98, AL 0·66–1·04 (30 measured).

Mandibles striate, armed with 4 teeth. Anterior clypeal margin usually shallowly concave, sometimes more or less straight, with a narrow apron and bounded on each side by a denticle or prominence where the anterior apron meets the longitudinal edges or carinae which bound the side of the median portion of the clypeus (Fig. 8). In most samples a definite denticle or sharp angular projection is visible on each side of the median clypeal margin but in a few, usually larger individuals, only a pair of low and bluntly rounded prominences occur. Maximum diameter of eye 0·18–0·26 (0·27–0·30 × HW). Anterior pronotal corners armed with a pair of flattened triangular teeth. Promesonotal shield basically as shown in Figs 23–25, narrowing behind the pronotum and without thin-spots or fenestrae. Promesonotal suture usually absent but sometimes visible as a narrow transverse line. Posterior corners of mesonotum armed with a pair of spines which are very variable in length and thickness, the posterior mesonotal margin between the spines concave and without secondary armament in the form of prominences or teeth. A lamina usually present on the posterior mesonotal margin between the spines, which is very variable in development; in most it is a narrow strip or is crescent-shaped but in others, particularly those samples with longer mesonotal spines, it may be extensive. Only rarely is this lamina so narrow as to be unapparent. Propodeum armed with a pair of long spines at about the level of the spiracle. Petiole in profile cuneate, broadest basally and narrowing above. Postpetiole nodiform. Dorsum of head usually densely longitudinally rugulose with numerous cross-meshes and with a reticulum occipitally. In some the entire head appearing reticulate-rugulose. Promesonotal shield and dorsum of postpetiole reticulate-rugulose, usually densely so. First gastral tergite with sculpture varying from a fine dense shagreening to a conspicuously reticulate-punctate surface. Most commonly the sculpture is stronger and more conspicuous on the basal part of the tergite, and tends to be reduced or to fade out more apically on the segment. All dorsal surfaces of the head and body with a dense pelt of soft curved hairs. Colour medium to dark brown, usually with the gaster darker in shade than the head and alitrunk; sometimes with a reddish or foxy tint.

M. magrettii is primarily a savannah and open-woodland species of eastern and southern Africa. The Ghanaian records from Legon are from the coastal plain of that country which is also inhabited by numerous other typically savannah or grassland forms. This species is extremely variable in size, intensity of sculpture and in details of the shape of the promesonotal shield. It is true to say that no two series are exactly alike and the differences between the largest and smallest workers seem, at first glance, to indicate that more than one species is present. However, the existence of intermediates between almost all the variants has convinced me that only one species is in fact represented.

Diagnostic characters of *magrettii* include its 4-dentate mandibles, armed clypeal margin, form of the promesonotal shield and nodiform postpetiole.

MATERIAL EXAMINED

Ghana: Legon (*D. Leston*); Legon (*G. Beson*); Legon (*Mkhise*). **Sudan:** Torit (*N. A. Weber*); Equatoria (*N. A. Weber*). **Uganda:** Jinja (*N. A. Weber*). **Kenya:** Mombasa (*N. A. Weber*); Bissell (*J. Darlington*);

Shimba Hills (*B. Hölldobler*); Olkiloriti (*M. G. Lepage*); Kajiado (*G. Nyamasyo*). **Tanzania:** no loc. (*G. Loveridge*). **Botswana:** Maxwee (*A. Russell-Smith*); Xani Pan (*A. Russell-Smith*). **Zimbabwe:** Bulawayo (*G. Arnold*); Victoria Falls (*G. Arnold*); Hillside (*G. Arnold*); Broken Hill (*G. Arnold*); Sawmills (*G. Arnold*); Chishawasha (*A. Watsham*). **South Africa:** Transvaal, Pretoria (*J. C. Faure*); T., Pretoria, Magalieskraal (*Lingnau*).

Meranoplus peringueyi Emery

(Figs 6, 20–22)

Meranoplus peringueyi Emery, 1886: 365, pl. 17, fig. 12. Syntype workers, SOUTH AFRICA: Cape of Good Hope (*L. Peringuey*) (MRAC, Tervuren; MCSN, Genoa; MHN, Geneva; NM, Basle [examined].

Meranoplus excisus Arnold, 1914: 29, fig. 9. Syntype workers, SOUTH AFRICA: Natal, Estcourt (*R. C. Wroughton*) (BMNH; NM Bulawayo) [examined]. **Syn. n.**

WORKER. TL 3·2–4·9, HL 0·80–1·12, HW 0·74–1·10, CI 93–100, SL 0·52–0·74, SI 67–72, PW 0·70–1·10, AL 0·74–1·20 (20 measured).

Mandibles striate, armed with five teeth. Median portion of clypeus narrowing anteriorly, the margin with a narrow apron or without a distinct apron. Lateral carinae of median portion of clypeus continuous with the anterior margin, without a prominence or denticle where they meet. Maximum diameter of eye 0·17–0·26 (0·21–0·24 × HW). Promesonotal shield strongly marginate and overhanging the sides and propodeum, but the long propodeal spines always visible projecting below the posterior mesonotal margin. Anterior pronotal corners armed with teeth or short triangular spines. Posterior mesonotal corners with a pair of spines and the posterior mesonotal border between these spines with a pair of broad triangular teeth which are variable in shape and size. Promesonotal suture usually absent but sometimes visible as a faint line traversing the shield. Promesonotal shield on each side, at the site of the junction of pro- and mesonotum, with a thin spot which usually extends outwards to the lateral margin. This is usually quite obvious but may be inconspicuous in some workers, especially larger individuals. Commonly the lamella of the thin-spot eroded, to a greater or lesser degree, from the margin inwards, and in general the greater the erosion of the thin-spot the more the mesonotal margin behind the spot projects outwards (Figs 20–22). Propodeum armed with a pair of long stout spines. Petiole in profile cuneate, tapering from a broad base to a crest-like apex. Postpetiole strongly nodiform. Dorsum of head rugose, usually strongly so; most commonly the longitudinal component of the rugosity predominates and in some samples the head is almost entirely longitudinally sculptured. In general, however, there are several to many cross-meshes present and some individuals have the entire head reticulate-rugose. Promesonotal shield and dorsum of postpetiole reticulate-rugose. First gastral tergite densely finely punctulate or shagreened, at least basally, often the sculpture extending over the whole sclerite. All dorsal surfaces of head and body, and the scapes and tibiae, with a dense pelt of fine soft hairs. Colour uniform medium brown to blackish brown.

A very distinctive species known only from Lesotho and South Africa, *peringueyi* is separated from all its African congeners by its combination of 5 mandibular teeth, unarmed clypeal margin and petiole, nodiform postpetiole and long propodeal spines.

MATERIAL EXAMINED

Lesotho: Qathas Nek (*G. Arnold*). **South Africa:** Cape Province, Katberg (*R. E. Turner*); C. P., Worcester (*R. E. Turner*); C. P., Willowmore (*G. Arnold*); C. P., Willowmore (*W. L. Brown*); C. P., Bethlehem (*Merve*); C. P., Cape of Good Hope (*G. B. King*); C. P., Van Rhyns Pass (*A. Mackie*); C. P., Doorn River (*A. Mackie*); C. P., Port Elizabeth (ex coll. Mayr); C. P., Grahamstown (*W. L. Brown*); Natal (*Wroughton*); Natal, Drakensberg, Mts, Little Berg (*G. Arnold*).

DICROASPIS Emery **stat. rev.**

(Figs 26, 27)

Dicroaspis Emery, 1908: 184. Type-species: *Dicroaspis cryptocera* Emery, op. cit.: 185, by monotypy.

Dicroaspis Emery; Emery 1915: 15, and all subsequent authors. [As subgenus of *Calyptomyrmex*.]

Geognomicus Menozzi, 1924: 220. Type-species: *Geognomicus wheeleri* Menozzi, loc. cit. [=*Dicroaspis cryptocera* Emery], by original designation. **Syn. n.**

DIAGNOSIS OF WORKER. Myrmicine ants with triangular mandibles whose apical (masticatory) margins are armed with 7–8 small, spaced-out teeth. Palp formula 2,2 based on an *in situ* count. (Maxillary palp apparently has a large basal and much smaller apical palpomere; the labial palp has two conspicuous large segments.) Clypeus with a narrow anterior apron which overhangs the basal margins of the mandibles. Median portion of clypeus behind the anterior margin vertical or nearly so, terminating above in a projecting biramous appendage or fork; this clypeal fork almost on a level with the frontal lobes and projecting out over the basal portions of the mandibles. Frontal lobes strongly expanded and overhanging the anterior clypeal apron. Posteriormost part of the clypeus, behind the clypeal fork, very narrow and deeply inserted between the frontal lobes. Antennae with 11 segments, the 3 apical flagellomeres forming a strong club. Scapes not strongly incrassate in their distal halves. Antennal scrobes present, extensive and deep, running back well beyond the level of the eye, bounded above by the posteriorly-divergent frontal carinae and below by a ridge running above the eye. Frontal carinae not strongly expanded laterally over the scrobes so that most of the scrobal concavity is clearly visible in dorsal view. Promesonotum forming a single convexity in profile. Propodeum sloping steeply, armed with a pair of short, stout spines. Metapleural lobes rounded. Petiole with a short, very thick and dorsally very broad anterior peduncle, with a ventral process present anteriorly. Petiole node low and rounded, tapering dorsally from a broad base. Postpetiole with an anterior process ventrally which appears as a broad tooth in profile but which is seen to be a broad transverse flange or lip in anterior view, running the width of the segment. First gastral tergite large, projecting much further than the first sternite and weakly vaulted apically so that the remaining tergites are reflexed and the sting orifice is ventrally situated. Pilosity dense, the hairs simple and fine; without bizarre pilosity.

When Emery (1908) first described *Dicroaspis* he treated it as a good genus, closely related to *Calyptomyrmex* but separated from it by a reduced antennomere count, the shape of the head and the presence of simple, as opposed to bizarre, pilosity.

Between 1908 and 1915 a few *Calyptomyrmex* species were described as having 11 antennal segments rather than 12 and this apparently convinced Emery that his *Dicroaspis* was best treated as a subgenus of *Calyptomyrmex,* as the two seemed to be separable only by a one-segment difference in antennomere count. Thus in 1915 he reduced *Dicroaspis* to subgeneric status under *Calyptomyrmex.*

The present study has shown that those *Calyptomyrmex* species for which an 11-merous count was claimed, and which were consequently placed in subgenus *Dicroaspis* (*arnoldi, clavisetus, foreli, pusillus*) were all based on miscounts of the narrow annular segments of the antennae; in fact all of these species, and all known *Calyptomyrmex* species to date, have 12-segmented antennae.

Having removed these species back to *Calyptomyrmex* proper only *cryptocera* and *laevidens* remained in *Dicroaspis,* which then seemed best treated as a separate genus on the diagnostic characters given above and the differences from *Calyptomyrmex* tabulated below. There remained only the anomalous monotypic genus *Geognomicus* to deal with, as from its description it seemed related to both *Dicroaspis* and *Calyptomyrmex.* Examination of the type of *Geognomicus wheeleri,* (type- and only species of the genus) showed that it was a direct synonym of *Dicroaspis cryptocera,* and thus *Geognomicus* sank automatically into the synonymy of *Dicroaspis.*

Characters separating *Calyptomyrmex* and *Dicroaspis* are as follows; the first three characters and the final one are the most important.

Calyptomyrmex	*Dicroaspis*
Antennae with 12 segments (Fig. 28).	Antennae with 11 segments (Fig. 27)
Scapes strongly expanded and incrassate in apical half, with a narrow projecting flange on the leading edge.	Scapes thicker distally but not strongly expanded nor incrassate in apical half, without a projecting flange on the leading edge.
Petiole in profile with a long narrow anterior peduncle, without a large anteroventral process (Figs 33–40).	Petiole in profile with a short and very stout anterior peduncle, with a large anteroventral process (Fig. 26).
Node of petiole high, not narrowing above.	Node of petiole low, narrower above than below.

Calyptomyrmex	*Dicroaspis*
Anterior subpostpetiolar process a tooth on each side (in all African species).	Anterior subpostpetiolar process a transverse ridge or flange.
Gastral tergites 2 to apex not reflexed ventrally.	Gastral tergites 2 to apex relfexed ventrally.
Head in dorsal view with frontal carinae strongly expanded, concealing most or all of the scrobal area.	Head in dorsal view with frontal carinae not strongly expanded, most of the scrobal area clearly visible.
Body partially or entirely with bizarre pilosity.	All body hairs fine and simple.

The two known species of *Dicroaspis* are restricted to Central Africa, having been recorded from Gabon, Zaire and Principe I. to the present. They are obviously related to the members of *Calyptomyrmex* but the construction of the petiole resembles strongly that seen in the minute species of *Mayriella* from Nepal, the Indo-Australian region and Australia.

The two presently recognized species of *Dicroaspis* are both based on relatively little material and may prove to be variants of a single form. However, for now I propose to treat *laevidens* as a good species, separating it from *cryptocera* by the characters given in the key below.

Synonymic list of species

cryptocera Emery
  wheeleri Menozzi **syn. n.**
laevidens (Santschi) **stat. n.**

Key to species (workers)

1 Piligerous punctures on basal portion of first gastral tergite effaced, barely visible. Propodeal dorsum in profile without a peak in the outline before sloping to the spines. Slightly larger species, HL 0.80–0.86, AL 0.86–0.92. (Zaire, Principe I.)... ***cryptocera*** (p. 58)

Piligerous punctures on basal portion of first gastral tergite coarse, broad and conspicuous. Propodeal dorsum in profile with a peak in the outline before sloping to the spines (Fig. 26). Slightly smaller species, HL 0.72, AL 0.74. (Gabon, Zaire)... ***laevidens*** (p. 59)

Treatment by species

Dicroaspis cryptocera Emery

Dicroaspis cryptocera Emery, 1908: 185, fig. 1. Syntype worker, female, ZAIRE: Stanleyville (=Kisangani) (*H. Kohl*) (MCSN, Genoa) [worker examined].

Calyptomyrmex (*Dicroaspis*) *cryptocerus* (Emery); Emery, 1915: 15, and all subsequent authors.

Geognomicus wheeleri Menozzi, 1924: 220, figs 1–3. Syntype workers, PRINCIPE I.: Roca Infante Don Enrique, 1.iii.1901, 100–300 m (*L. Fea*) (IE, Bologna [examined]. **Syn. n.**

WORKER. TL 3·0–3·1, HL 0·80–0·86, HW 0·68–0·74, CI 85–86, SL 0·50–0·56, SI 74–77, PW 0·50–0·54, AL 0·86–92 (3 measured).

Mandibles smooth with a few scattered small pits. Anterior clypeal margin transverse, concealing the basal mandibular teeth when the latter are closed. Narrow vertical median portion of clypeus below the fork transverse and unsculptured. In dorsal view the clypeal fork short, the distance across the apices of its teeth exceeding the length of the side of the fork from apex to frontal lobe. Narrow median portion of clypeus (running back between the frontal lobes) smooth and very shiny. Frontal lobes strongly expanded, convergent posteriorly to the bases of the frontal carinae; the latter divergent and running back almost to the occipital margin, each with a narrow laterally projecting flange along most of the length. Antennal scapes with the distal two-thirds thicker than the proximal third but not incrassate and lacking any lamelliform extension of the leading edge. Eyes small, maximum diameter 0·07–0·08 (0·10–0·11 × HW), with 3–4 ommatidia in the longest row; the eyes situated below the scrobe and separated from its strong ventral margin by a distance about equal to their maximum diameter. Promesonotum forming a single convexity in profile, the metanotal groove very shallowly marked. Propodeal dorsum with a short, more or less flat portion behind the metanotal groove and then sloping steeply to a pair of short, stout triangular spines. Metapleural lobes narrow but deep, evenly rounded and running from the base of the spine almost to the metapleural angle. Short thick peduncle of petiole equipped anteroventrally with a broad, keel-like process which projects forwards and is concealed by the metapleuron and its lobes unless the pedicel segments are raised. Node of petiole with the anterior and posterior faces converging dorsally so that the dorsal surface is short. Structure of postpetiole, gaster and other major characters as described under the generic diagnosis. Dorsum of head and promesonotum rugose, the rugae low and rounded, not sharply defined. On the head the rugae predominantly or entirely longitudinal but with a tendency to meander. On the promesonotum in places the rugae enclose foveolate spaces. Scrobal areas unsculptured, smooth and shining. Propodeum with a transverse line or ridge between the spines which marks the true junction of dorsum and delivity; both the sloping dorsum above the line and the declivity below it smooth and highly polished. First gastral tergite with piligerous punctures faint to effaced, difficult to discern. All dorsal surfaces of head and body with numerous short, fine curved simple hairs. Colour glossy light reddish brown.

Known only from the type-series of *cryptocera* and its synonym *wheeleri,* this species seems to be restricted to Central Africa.

Dicroaspis laevidens (Santschi) **stat. n.**

(Figs 26, 27)

Calyptomyrmex (*Dicroaspis*) *cryptocerus* var. *laevidens* Santschi, 1919: 88. Syntype workers, ZAIRE: Yambuya, 26.xi.1913, no. 83 (*Bequaert*) (MRAC, Tervuren; NM, Basle) [examined].

WORKER. TL 2·5–2·6, HL 0·72, HW 0·62–0·64, CI 86–88, SL 0·44–0·46, SI 72–73, PW 0·46–0·48, AL 0·74 (2 measured).

Gross characters as given under the generic diagnosis and answering to the description of *cryptocera,* but with the differences noted in the key.

Apart from this *laevidens* is a somewhat smaller (compare measurements), more heavily sculptured version of *cryptocera.* Sculptural differences are in intensity rather than form; on the promesonotum the low rugae tend to enclose numerous reticular spaces or foveolate spaces, and on the first gastral tergite the piligerous punctures form broad but shallow conspicuous pits. Eye-size is about the same as in *cryptocera,* with maximum diameter 0·06 (0·09–0·10 × HW), with 3 ommatidia in the longest row.

These differences are apparently minor but, because so few specimens of either species are known, I have decided to treat them as being significant at species-level until more material becomes available. Nevertheless, a strong suspicion remains that only a single species may be represented here.

MATERIAL EXAMINED
Gabon: Plateau d'Ipassa (*J. A. Barra*). **Zaire:** Yangambi (*M. Maldague*).

CALYPTOMYRMEX Emery

(Figs 28–44)

Calyptomyrmex Emery, 1887: 471. Type-species: *Calyptomyrmex beccarii* Emery, op. cit.: 472, by monotypy.

Weberidris Donisthorpe, 1948: 281. Type-species: *Weberidris rufobrunnea* Donisthorpe, loc. cit., by original designation. [Synonymy by Brown, 1949: 84.]

DIAGNOSIS OF WORKER. Myrmicine ants. Mandibles triangular with 6–8 teeth arrayed on a fairly long masticatory margin; usually with 6 teeth but counts of 7 or 8 have been noted in a few species (*nummuliticus, rennefer, piripilis*). Behind the apical the teeth are usually widely spaced and commonly the gaps between teeth are greater than the lengths of the teeth themselves. Palp formula 2,2 (dissections of *barak, brevis, kaurus, nummuliticus, piripilis, rennefer, shasu,* plus two extralimital species), always with the basal maxillary palpmere very short and inconspicuous. Clypeus with a narrow anterior apron which overhangs the basal margins of the mandibles. Median portion of clypeus behind the anterior margin vertical or nearly so, terminating above in a projecting biramous appendage (the clypeal fork) which projects out over the mandibles and partially conceals them in dorsal view (Fig. 28). Frontal lobes strongly expanded and overhanging the anterior clypeal margin. Posteriormost part of the clypeus, behind the clypeal fork, narrow and deeply inserted between the frontal lobes. Antennae with 12 segments, the three apical flagellomeres forming a stout club; flagellomeres 2–8 usually reduced to narrow annuli. Scapes strongly incrassate in their distal halves, with a narrow projecting lamina on the leading edge of the incrassate portion. Antennal scrobes extensive and deep, bounded above by the strong frontal carinae and below by a ridge running above the eye, the scrobes capable of accommodating the whole antenna. Promesonotum forming a single convexity in profile which is elevated above the level of the sloping propodeum (Figs 33–40), the latter usually armed with denticles or teeth but unarmed in several species. Metapleural lobes prominent and rounded, usually with a more or less central thin-spot. Petiole in profile with an elongate fairly narrow peduncle which lacks a ventral process, and with a conspicuous large node. Postpetiole in profile with a broad and usually blunt tooth-like ventral process. First gastral tergite large but not vaulted apically. Some or all dorsal surfaces of the body with bizarre pilosity.

With the removal of the true members of *Dicroaspis* from *Calyptomyrmex* (see above), and the discovery that others formerly placed in *Dicroaspis* (*arnoldi, clavisetus, foreli,* and the now-synonymized *pusillus*) have 12 antennal segments rather than 11 as was originally stated for each of them, what remains under *Calyptomyrmex* now forms a compact genus. At present 25 species have been described, 16 of which occur in the Ethiopian zoogeographical region. The six species of the Oriental region/western Indo-Australian region have recently been revised by Urbani (1975), and of the final three species two occur in New Guinea and one in Australia.

All members of the genus are typically found in leaf-litter, humus and topsoil and nest either directly into the earth or into rotten wood embedded in the topsoil. Foraging is carried out by individuals or by two to three workers together. Many of the species 'play dead' when disturbed or freeze and remain motionless for several moments, usually blending in very well with the background.

The female (queen) caste is known for six African species and at least one extralimital form. Most of these are normal alates but two of the African species appear to have highly ergatoid females; these are discussed under *piripilis,* one of the species in which such ergatoids occur. In general the females fit the description of the worker given above, differing only in the usual characters of possessing ocelli, having expanded alitrunks with a full complement of flight sclerites, and being larger. Males are very rarely collected and in consequence virtually unknown. Associated males are known only of the African species *nummuliticus* and *foreli,* and for the Australian species *schraderi* Forel where they form part of the type-series. For the record, males of *nummuliticus* are housed in BMNH and MCZ, Cambridge and originate in Ivory Coast and Nigeria; males of *foreli* from South Africa are preserved in NM, Bulawayo.

One striking character shown by the members of *Calyptomyrmex* is the universal presence of bizarre pilosity. This occurs on all dorsal surfaces of the head and body but is always absent from the propodeal dorsum (one or two hairs may occur marginally but never on the dorsum proper). These bizarre hairs may be scale-like, tear-drop shaped, spatulate, clavate, or truly weird such as the hairs described for *stellatus.* Even in forms such as *barak,* where the hairs are described as simple, they are not the usual simple hairs seen so widely in the ants but rather are short, very stout, and taper to an abrupt point. I am baffled by the diversity of these bizarre hairs and can offer no explanation as to their function.

Synonymic list of species

barak-group
- ***barak*** **sp. n.**

piripilis-group
- ***brevis*** Weber
- ***kaurus*** **sp. n.**
- ***piripilis*** Santschi
    - *cataractae* Arnold **syn. n.**
    - *cataractae* subsp. *litoralis* Arnold **syn. n.**
    - *punctatus* Weber **syn. n.**

arnoldi-group
- ***arnoldi*** (Forel)
- ***foreli*** Emery
    - *emeryi* Forel (homonym)
    - *pusillus* Santschi **syn. n.**
    - *arnoldi* subsp. *hartwigi* Arnold **syn. n.**
- ***nedjem*** **sp. n.**
- ***nummuliticus*** Santschi
    - *reticulatus* Weber **syn. n.**
- ***stellatus*** Santschi

brunneus-group
- ***brunneus*** Arnold
- ***clavatus*** Weber
- ***clavisetus*** (Santschi)
- ***duhun*** **sp. n.**
- ***rennefer*** **sp. n.**
- ***shasu*** **sp. n.**
- ***tensus*** **sp. n.**

Key to species (workers)

1 Hairs on first gastral tergite scale-like and with the outer edge of each hair having 15–20 freely projecting short filaments so that the margin of the hair has a fringed or ray-like appearance. (Gabon) . . . . ***stellatus*** (p. 69)

– Hairs on first gastral tergite variously shaped, sometimes scale-like but never with the outer edge of each hair with freely projecting filaments giving a fringed or ray-like appearance. 2

2 Hair closest to apex on outer margin of clypeal fork short, stout and conspicuously thickened, usually blunt, contrasting strongly with the fine hairs which project forward from the vertical face of the clypeus below the fork (Fig. 44). Hairs on outer margin of fork behind the apicalmost always stout and like the apicalmost hair 3

– Hair closest to apex on outer margin of clypeal fork elongate, simple and fine, similar in structure to the fine hairs which project forward from the vertical face of the clypeus below the fork, but shorter (Fig. 43). Hairs on outer margin of fork behind the apicalmost either similar to the apicalmost or distinctly thickened as in Fig. 43 6

3 Maximum diameter of eye much greater (2–4 times greater) than the maximum width of the hairs in the first transverse pronotal row (Fig. 39) 4

– Maximum diameter of eye at most equal to the maximum width of the hairs in the first transverse pronotal row, usually distinctly less (Fig. 36) 5

4 Flattened hairs on first gastral tergite scale-like, short and squat, widely scattered (Fig. 30). (Zimbabwe) . . . . ***arnoldi*** (p. 66)

– Flattened hairs on first gastral tergite elongate and narrow, spatulate and with a tapering long basal stem, dense (Fig. 31). (Uganda) . . . . ***tensus*** (p. 74)

5 Eyes with 5–6 facets, maximum diameter c. 0·04, about 0·05–0·06 × HW. Smaller species, HW 0·62–0·68, AL 0·60–0·64. (Sudan, Ghana, Zaire) . . . . ***brevis*** (p. 63)

– Eyes with >6 facets, maximum diameter c. 0·06–0·08, about 0·08–0·10 × HW. Larger species, HW 0·68–0·80, AL 0·66–0·84. (Sudan, Kenya, Zaire, Zimbabwe, Angola, South Africa) . . . . ***piripilis*** (p. 65)

6 First gastral tergite without scale-like, spatulate or clavate hairs; all hairs erect, simple, stout and acute apically (Fig. 33). (Ivory Coast, Ghana, Nigeria, Gabon). . . . ***barak*** (p. 62)

– First gastral tergite with scale-like, spatulate or clavate hairs present 7

7 Maximum diameter of eye usually less than the maximum width of the hairs in the first transverse pronotal row, at most the widths about equal. (Ivory Coast, Ghana, Angola) ***kaurus*** (p. 64)

– Maximum diameter of eye distinctly greater than the maximum width of the hairs in the first transverse pronotal row 8

8 Bizarre hairs similar to those on first gastral tergite present everywhere on the first gastral sternite (Fig. 38) (Uganda, Tanzania, Burundi, Zaire) . . . . . . ***shasu*** (p. 73)

– Bizarre hairs similar to those on first gastral tergite restricted to the posterior one-third of the first gastral sternite or entirely absent from the first sternite 9

9 With first gastral tergite in dorsal view the hairs squamate, scale-like or tear-drop shaped, without a long tapering basal stem (Figs 29, 32, 34). 10

– With first gastral tergite in dorsal view the hairs not squamate, either elongate-clavate, long-spatulate or Indian club-shaped, with a long tapering basal stem (Figs 35, 37, 41, 42) . 12

10 Large species, HW 0·78–0·98, PW 0·54–0·68 with abundant large squamate hairs (Fig. 34). On the first gastral tergite the width of each hair about equal to or greater than the distance to the hairs on each side of it (Fig. 29). Mandibles longitudinally striate, usually sharply and conspicuously so. (Ivory Coast, Ghana, Nigeria, Cameroun, Zaire) . . ***nummuliticus*** (p. 68)

– Smaller species, HW 0·56–0·70, PW 0·40–0·50 with small squamate hairs. On the first gastral tergite the width of each hair distinctly less than the distance to the hairs on each side of it (Fig. 32). Mandibles smooth or with vestigial marking, not longitudinally striate 11

11 Dorsum of head predominantly longitudinally rugulose, with a reticulum occipitally but without a triangular area on the vertex which is transversely rugulose. (Zimbabwe) ***nedjem*** (p. 68)

– Dorsum of head with longitudinal rugulae on each side which diverge towards the occipital corners and enclose a roughly triangular area of the vertex which is predominantly or entirely transversely rugulose. (Ethopia, Gabon, South Africa). . . . ***foreli*** (p. 67)

12 Hairs on outer margin of clypeal fork behind the apicalmost hair as fine as the apicalmost, similar in appearance. Clavate hairs on first gastral tergite very long and slender, longer than the maximum diameter of the eye (Fig. 35). (Zaire) . . . . . ***rennefer*** (p. 72)

– Hairs on outer margin of clypeal fork behind the apicalmost hair much stouter than the apicalmost, very different in appearance. Clavate hairs on first gastral tergite stout, at most only slightly longer than the maximum diameter of the eye, usually shorter (Figs 37, 41, 42) 13

13 Propodeal dorsum strongly transversely rugose, without reticulate-punctate sculpture. Larger species, HW 0·76–0·82, PW 0·52–0·60. (Kenya, Uganda, Zaire) . . . . **duhun** (p. 72)

– Propodeal dorsum reticulate-punctate, without strong transverse rugae but sometimes with one or two very feeble irregular rugulae. Smaller species, HW 0·52–0·66, PW 0·34–0·50 . 14

14 Postpetiole in dorsal view distinctly broader and more massively developed than the petiole (Fig. 42). Eyes with 15 or fewer ommatidia 15

– Postpetiole and petiole in dorsal view of approximately equal widths, the former not obviously broader than the latter (Fig. 41). Eyes with 18 to >20 ommatidia. (Ethiopia, Kenya, Zaire) **clavatus** (p. 70)

15 Larger species, HW 0·64 or more, PW 0·48 or more. Prongs of clypeal fork long, their outer edges not strongly bowed outwards. (Zimbabwe, South Africa) . . . **brunneus** (p. 70)

– Smaller species, HW 0·52–0·60, PW 0·34–0·42. Prongs of clypeal fork short and stout, their outer edges strongly bowed outwards. (South Africa) . . . . . **clavisetus** (p. 71)

The species-groups

The 16 African species of *Calyptomyrmex* fall into four informal groups based on the form of the pilosity and the size of the eyes. The *barak*-group, containing only a single species, is characterized by its simple stout pilosity, all the hairs being short, thick and acutely pointed apically. All the other groups have much more bizarre pilosity, with squamate, spatulate or clavate hairs predominating. Members of the *piripilis*- and *arnoldi*-groups have gastral hairs which are scale-like or tear-drop-shaped, always strongly flattened and broad in dorsal view. In *piripilis* and its allies the eyes are very reduced, whilst in the *arnoldi*-group they are larger. A useful measure of the relative sizes of the eyes is to compare the maximum ocular diameter with the width of the hairs in the first transverse pronotal row, as usually both can be seen at the same time in a direct lateral view of the specimen. Thus in the *piripilis*-group the eyes at most only fractionally exceed the widths of these hairs and are usually smaller, whilst in the *arnoldi*-group the eyes are commonly 2–4 times wider than the hairs in the first pronotal row.

The final group, containing *brunneus* and its allies, has relatively large eyes as in the *arnoldi*-group but has the hairs on the first gastral tergite longer and narrower. These hairs are elongate-clavate, long-spatulate or Indian club-shaped, always with a long tapering basal stem.

The *barak*-group

(Figs 28, 33)

Hairs on all dorsal surfaces of the body erect, stout, straight and simple, tapering to a point apically; without squamate, spatulate, clavate or otherwise bizarre pilosity.

The single species referable to this group (*barak*) is a relatively large form (HW 1·00–1·08) apparently widely but sparsely distributed in West and Central Africa. To the present it is known from Ivory Coast, Ghana, Nigeria and Gabon. The samples from Ghana and Nigeria were found in rotten wood.

The simple form of the pilosity is diagnostic of *barak* and separates it from all other known African species. Outside the Ethopian region a similar form of pilosity occurs in *C. wittmeri* Urbani from Bhutan, and in an as yet unidentified species from Sarawak.

Calyptomyrmex barak sp. n.

(Figs 28, 33)

HOLOTYPE WORKER. TL 4·3, HL 1·04, HW 1·06, CI 102, SL 0·62, SI 58, PW 0·76, AL 1·14.

Mandibles finely but strongly longitudinally striate. Hair closest to apex on outer margin of clypeal fork, and all other hairs on clypeal fork, simple; similar in structure to the hairs projecting forwards from the vertical portion of the clypeus below the fork but shorter. Maximum diameter of eye 0·10 (0·09 × HW), much greater than the width of the hairs in the first pronotal row; with 5 ommatidia in the longest row and each eye with > 15 ommatidia in all. Propodeal declivity armed with a pair of triangular teeth. Metapleural lobes broadly rounded. Petiole node in profile massive, larger than the postpetiole node; in dorsal view both nodes distinctly broader than long, of approximately equal width. Dorsum of head finely and quite densely longitudinally rugulose, with a few weaker cross-meshes towards the occipital corners. The entire surface, including the top surfaces of the rugulae, covered by a dense blanketing fine reticulate-punctulation. Promesonotal dorsum finely but very irregularly rugulose, loosely reticulate in places and with the punctulate ground-sculpture distinctly weaker than on the head. Propodeum irregularly rugose anteriorly but transversely so between the propodeal teeth. Punctulate ground-sculpture virtually effaced on the dorsal propodeum. Nodes both rugulose and finely densely punctulate dorsally. First gastral tergite with a feeble superficial shagreening extending over the whole of the sclerite. Hairs on all surfaces of the head and body stout and simple, of approximately equal thickness throughout their length but tapering to a point apically. Squamate or clavate hairs entirely absent. Colour dark reddish-tinged brown, the appendages lighter.

PARATYPE WORKERS. TL 3·9–4·3, HL 0·98–1·06, HW 1·00–1·08, CI 102–104, SL 0·60–0·62, SI 56–60, PW 0·70–0·76, AL 1·06–1·14 (5 measured).

As holotype but some with the promesonotum more distinctly reticulate-rugulose, and the ground sculpture almost as strong as on the head. Number of cross-meshes on the occipital area of the head variable. The intensity of gastral sculpture varies noticeably. In general it is as in the holotype but it may be reduced to a weak superficial patterning or strengthened to a blanketing shallow reticulate-punctulation. Eyes with 5–6 ommatidia in the longest row, the maximum diameter 0·10–0·11 (0·09–0·11 × HW).

Holotype worker, **Ghana:** Baudua, 27.viii.1969, rotten stump (*D. Leston*) (BMNH).

Paratypes. **Ghana:** 3 workers with same data as holotype. **Nigeria:** 1 worker, Gambari, 20.vi.1969, rotten log (*B. Bolton*). **Gabon:** 1 worker, Plateau d'Ipassa, IPA 7 Cl (*J. A. Barra*). **Ivory Coast:** 1 female (queen), Divo, 18.iii.1963, rain for. litter (*L. Brader*). (BMNH; MCZ, Cambridge; NM, Basle.)

A very distinctive species which apparently nests in rotten wood, *barak* is unique in the African fauna of this genus as it is the only known species without clavate, squamate, spatulate or otherwise flattened hairs. All body hairs in *barak* are thick and very distinctive but are roughly cylindrical in section and taper to an acute point apically.

The *piripilis*-group

(Figs 36, 44)

First gastral tergite with broad scale-like hairs. Eyes small, their maximum diameter at most only equal to the width of the hairs in the first transverse pronotal row, usually smaller.

The three species of this group are all widespread and apparently quite successful in the Ethopian region. *C. brevis* is known from forests in Sudan, Ghana and Zaire; *kaurus* from Ivory Coast, Ghana and Angola; and *piripilis* from Sudan, Kenya, Zimbabwe, Angola and Zaire. All three species appear to nest in the soil.

C. kaurus is separated from the other two species by having the apicalmost hair on the clypeal fork fine and simple. In *brevis* and *piripilis* this hair is short and stout. The two last-named species form a close pair, differentiated on small differences in the eyes and in their respective sizes.

Calyptomyrmex brevis Weber

Calyptomyrmex (*Calyptomyrmex*) *brevis* Weber, 1943: 366, pl. 15, fig. 1. Syntype workers, SUDAN: Imatong Mts, Lotti Forest, 5.viii.1939, no. 1441 (*N. A. Weber*) (MCZ, Cambridge; BMNH) [examined].

WORKER. TL 2·5–2·6, HL 0·62–0·66, HW 0·62–0·68, CI 98–103, SL 0·34–0·38, SI 53–58, PW 0·42–0·48, AL 0·60–0·64 (8 measured).

Mandibles finely and densely longitudinally striate. Hair closest to apex on outer margins of clypeal fork short and stout, contrasting with the long fine hairs which project forwards from the vertical face of the clypeus below the fork. Other hairs on the clypeal fork behind the apicalmost also short and stout, similar to the apicalmost. Eye very small, at most with 6 facets, its maximum diameter c. 0·04 (0·05–0·06 × HW), less than the width of the flattened hairs in the first transverse pronotal row. Propodeum in profile with merely an obtuse angle between the sloping dorsum and the declivity proper, or with a very low obtuse prominence, without denticles or teeth developed. Postpetiole slightly larger than petiole in dorsal view but not remarkably so. Dorsum of head finely and irregularly longitudinally rugulose, commonly with a reticulum occipitally; spaces between rugulae with a dense but shallow reticulate-punctulate ground-sculpture. Dorsal alitrunk irregularly rugulose, the constituents forming a loose broad-meshed reticulum in places. Propodeal dorsum shagreened to finely punctulate, often with a few feeble rugulae. Dorsal surfaces of nodes shagreened to finely punctulate, in general with a few weak rugulae but these may be absent. First gastral tergite feebly sculptured basally with superficial punctulation or shagreening which tends to be reduced or to fade out more posteriorly on the sclerite. All dorsal surfaces of body except propodeum liberally covered with large squamate hairs which are very conspicuous; those on the promesonotum arranged in 4–5 transverse rows, commonly the rows more even anteriorly than posteriorly where extra hairs are often seen between rows. Colour uniform light to medium brown.

Of the three species in this group *kaurus* is separated by having the apicalmost hair on the clypeal fork long and fine; it is short and thick in *brevis* and *piripilis*. These last two are closely related and it is possible that they may represent variants of a single species. However, in the material presently available they separate on the size of the eyes and bodily dimensions, as noted in the key.

Besides *brevis* and *piripilis*, three other African species are known in which the apicalmost hair on the clypeal fork is stout and thick. These are *stellatus* which is immediately characterized by its remarkable pilosity, and *tensus* and *arnoldi*, in both of which the eyes have a maximum diameter much greater than the width of the hairs in the first pronotal row (compare Figs 36, 39).

MATERIAL EXAMINED

Ghana: Tafo (*B. Bolton*), Tafo (*D. Leston*). **Zaire:** Ituri Forest, Beni-Irumu (*N. A. Weber*).

Calyptomyrmex kaurus sp. n.

HOLOTYPE WORKER. TL 2·4, HL 0·64, HW 0·66, CI 103, SL 0·36, SI 55, PW 0·44, AL 0·60.

Mandibles finely longitudinally striate. Hair closest to apex on outer margin of clypeal fork long and fine, similar in construction to the long hairs which project from the vertical face of the clypeus below the fork, but shorter. Hairs on outer margin of fork behind the apicalmost hair shorter and much stouter, contrasting strongly with the apicalmost. Eyes small, maximum 0·05 (0·08 × HW), equal to or slightly less than the width of the flattened hairs in the first transverse pronotal row. Propodeum in profile with an obtuse angle separating the sloping dorsum from the declivity proper, without teeth. Postpetiole slightly longer and broader than petiole in dorsal view, but not markedly so. Dorsum of head finely, irregularly, predominantly longitudinally rugulose; occipitally with a fine ruguloreticulum. Spaces between the rugulae granular or finely superficially punctulate, dull. Dorsal promesonotum finely and quite densely rugulose, the sculpture predominantly longitudinal, meandering and forming reticular meshes in places. Propodeal dorsum finely and densely punctulate, with granular or shagreened appearance, with a couple of very faint longitudinal weak rugulae. Petiole and postpetiole rugulose and finely punctulate dorsally, the first gastral tergite superficially shagreened everywhere. All dorsal surfaces of head and body except propodeum with abundant large, conspicuous, scale-like hairs which are, however, longer than broad. Colour uniform medium brown.

PARATYPE WORKERS. TL 2·4–2·8, HL 0·64–0·72, HW 0·66–0·72, CI 100–103, SL 0·36–0·42, SI 53–59, PW 0·44–0·52, AL 0·60–0·74 (12 measured).

Maximum diameter of eye 0·05–0·06 (0·07–0·09 × HW), generally smaller than the width of the hairs in the first pronotal row but sometimes about equal in width; the eye with 6–8 ommatidia. Hairs on promesonotal dorsum arranged in 5–6 transverse rows; behind the first two there are often hairs outside the rows and the pattern is disrupted. In some the promesonotum is more obviously reticulate-rugulose than in the holotype, and the propodeal dorsum may have several faint rugulae present. The propodeum in profile may develop minute low denticles instead of being merely angular, but teeth are never present.

Holotype worker, **Ghana:** Tafo, 29.x.1970, in leaf mould (*B. Bolton*) (BMNH).

Paratype workers. **Ghana:** 1 worker with same data as holotype; 1 worker, Kibi 24.iii.1970, litter sample (*D. Leston*). **Ivory Coast:** 5 workers, Nzi Noua, N. of Ndouci, 13.i.1977, degraded for., rot. log (*W. L. & D. E. Brown*); 1 worker, 3.5 km S. of Sangrobo, S-P de Tiassalé, 14.i.1977, rain for. (*W. L. & D. E. Brown*). **Angola:** 9 workers, Duque de Bragança falls, 12.iii.1972 (*P. M. Hammond*). (BMNH; MCZ, Cambridge; NM, Basle; NM, Bulawayo).

The combination of striate mandibles, small eyes, large squamate hairs and fine apicalmost hair on the clypeal fork will separate *kaurus* from all other species in the region.

Calyptomyrmex piripilis Santschi

(Figs 36, 44)

Calyptomyrmex piripilis Santschi, 1923: 282. Holotype worker, ZAIRE: Manyema, Niemba-Tengo (*Gérard*) (MRAC, Tervuren) [examined].

Calyptomyrmex cataractae Arnold, 1926: 283. Holotype worker, ZIMBABWE: Victoria Falls, rainforest, 30.viii.1917 (*G. Arnold*) (NM, Bulawayo) [examined]. **Syn. n.**

Calyptomyrmex cataractae subsp. *litoralis* Arnold, 1948: 221. Syntype workers, SOUTH AFRICA: Natal, Zululand, Richards Bay, ii.1946 (*J. C. Faure*) (NM, Bulawayo) [examined]. **Syn. n.**

Calyptomyrmex (*Calyptomyrmex*) *punctatus* Weber, 1952: 24, figs 19, 21, 23. Holotype worker, KENYA: 1°25'S 35°10'W [sic] to 1°38'S, 35°17'E, 4.ii.1948, no. 2039 (*N. A. Weber*) (AMNH, New York) [examined]. **Syn. n.**

WORKER. TL 2·8–3·1, HL 0·68–0·80, HW 0·68–0·79, CI 97–103, SL 0·38–0·48, SI 54–60, PW 0·46–0·54, AL 0·66–0·84 (15 measured).

Mandibles finely longitudinally striate. Hair closest to apex on outer margin of clypeal fork short and stout, contrasting strongly with the elongate fine hairs which arise from the vertical face of the clypeus below the fork. Hairs on clypeal fork behind the apicalmost all short and stout, similar in structure to the apicalmost. Eyes small, maximum diameter 0·06–0·08 (0·08–0·10 × HW), at most as large as the width of the hairs in the first transverse pronotal row, usually smaller then those hairs; the eyes with more than 6 facets. Propodeum in profile at most with a pair of minute obtuse prominences where the sloping dorsum meets the declivity, more commonly merely bluntly angled; without teeth. Petiole and postpetiole in dorsal view of approximately equal size, the two usually being about equal in length and width, but sometimes the latter fractionally broader than the former. In profile the petiole node usually appears larger than that of the postpetiole. Dorsum of head finely and usually quite densely irregularly longitudinally rugulose, the rugulae varying in density and intensity between series. Occipital region commonly with some cross-meshes, often with a loose reticulum. Spaces between the rugulae filled with fine dense punctulation or granulation, matt. Promesonotal dorsum finely irregularly rugulose, the sculpture often forming large reticular meshes, especially anteriorly. Propodeal dorsum reticulate-punctulate, sometimes with only this sculpture present but commonly with a few feeble rugulae superimposed upon the punctures. Petiole and postpetiole finely rugulose and punctulate dorsally. First gastral tergite finely densely punctulate or shagreened, at least basally, usually the entire sclerite similarly sculptured. All dorsal surfaces of head and body except the propodeum with numerous scale-like hairs which are very conspicuous; those on the promesonotum arranged in 4–5 transverse rows. Colour uniform light to medium brown.

One of three species in the region characterized by having relatively small eyes and large flattened scale-like hairs, *piripilis* is closely related to *kaurus* and *brevis*. It separates easily from *kaurus* as the anteriormost hair on the clypeal fork is simple in that species but short and greatly thickened in *piripilis*. Separation of *brevis* from *piripilis* rests on relative sizes of the eyes and dimensions of the body, as given in the key.

C. piripilis is a widespread species, ranging from Sudan to South Africa and also occurring in Angola and Zaire, but seeming to be absent from West Africa.

The female (queen) of this species appears to be ergatoid as a series in MCZ, Cambridge collected by W. L. Brown in Zimbabwe (Victoria Falls, spray forest, 7.iii.1969, no. R-14) contains 17 workers plus one odd larger specimen in which the mesonotum is strongly swollen, the promesonotal suture is present, and the eyes are very large; ocelli and flight sclerites are absent, however. Very little is known about the females of this genus but normal alate queens (with fully developed flight sclerites and ocelli) have been found in *nummuliticus, barak, clavatus* and *shasu*. The possibility that the ergatoid female noted above may in fact be a pathologically deformed worker cannot be absolutely ruled out, but the presence of a similar form in *rennefer*, with the additional character of having ocelli present, seems to indicate that ergatoid females may be usual in at least some species of *Calyptomyrmex*.

MATERIAL EXAMINED

Sudan: Imatong Mts (*N. A. Weber*). **Kenya:** 1°25'S 35°10'W [sic], to 1°38'S 35°17'E (*N. A. Weber*). **Zaire:** P.N.A., Mont. Ngulingo, Nyamgaleke (*P. Vanschuytbroeck*); Mt Hoyo, grotte Saga-Saga and grotte Tala-Tala (*P. Vanschuytbroeck*); Secteur Nord, Kavudula, Kilia (*P. Vanschuytbroeck*); riv. Sumalebu, Djuma (*P. Vanschuytbroeck*); Tungula, Semliki (*P. Vanschuytbroeck*); Kilebu, Abyalose (*P. Vanschuytbroeck*).

Angola: Gabela (*D. Hollis*). **Zimbabwe:** Victoria Falls (*W. L. Brown*). **South Africa:** Natal, Mtunzini (*J. C. Faure*).

The *arnoldi*-group

(Figs 29, 30, 32, 34, 39)

First gastral tergite with hairs scale-like or short, broadly tear-drop-shaped; without a long tapering basal stem. Maximum diameter of eye greater than width of hairs in first transverse pronotal row.

This group includes five species, namely *arnoldi, foreli, nedjem, nummuliticus* and *stellatus*. The known distribution of most of these is very limited, with *stellatus* known only from Gabon, and *arnoldi* and *nedjem* only from Zimbabwe. *C. foreli* is more widespread but equally rare, being known from the three very widely separated countries of Ethiopia, South Africa and Gabon. Finally, *nummuliticus* is fairly common in West Africa and also occurs in Cameroun and Zaire, where it is a wet-forest species.

C. stellatus is instantly recognizable by its unique pilosity. All the scale-like hairs on the dorsum are flattened and fringed with radiating filaments. Of the remaining species *arnoldi* is the only one which has the apicalmost hairs on the clypeal fork stout and thick; and *foreli* is characterized by having an area of the vertex transversely sculptured. *C. nedjem* and *nummuliticus* lack the characters diagnostic of the above; the latter is a large, darkly coloured species with striate mandibles and large scale-like hairs all over the body, whilst *nedjem* is a smaller, lightly coloured species with smooth mandibles and much smaller scale-like hairs.

Calyptomyrmex arnoldi (Forel)

(Figs 30, 39)

Dicroaspis arnoldi Forel, 1913: 115. Syntype workers, ZIMBABWE: Bulawayo, 20.iv.1912, 'under a stone with *P. krugeri* For.' (*G. Arnold*) (MHN, Geneva; BMNH) [examined].
Calyptomyrmex arnoldi (Forel) Arnold, 1917: 360.

WORKER. TL 2·5–2·7, HL 0·64–0·70, HW 0·64–0·68, CI 97–100, SL 0·38–0·42, SI 59–62, PW 0·46–0·52, AL 0·66–0·74 (6 measured).

Mandibles usually delicately and faintly striate, rarely more or less smooth. Clypeal fork relatively broad, distance between points of fork greater than outer length from apex to frontal lobe. Erect hair closest to apex on outer margin of clypeal fork stout and thick, contrasting with the long fine hairs which project forward from the vertical part of the clypeus below the fork. Outer margin of clypeal fork with at least one other erect thick hair behind the apicalmost. Eyes relatively large, maximum diameter c. 0·08 (0·12–0·13 × HW), much greater than the width of the flattened hairs on the first pronotal row and usually >10 ommatidia. Propodeum in profile armed with a pair of short conspicuous triangular teeth. Metapleural lobes with a conspicuous thin-spot. Node of petiole in profile usually slightly higher than that of postpetiole and commonly somewhat more voluminous. In dorsal view the two nodes are approximately equal in width or the postpetiole is slightly broader than the petiole. Dorsum of head with fine irregular scattered rugulae which usually tend to diverge towards the occipital corners. Scattered irregular cross-meshes may occur on the head, and are usually present occipitally where they sometimes from a loose reticulum. Spaces between rugulae densely shagreened or densely finely reticulate-punctulate, matt and dull. Promesonotum sculptured as head, with scattered irregular rugulae which may form a reticulum in places and with dense punctulation or shagreening between the rugulae. Propodeal dorsum predominantly or entirely reticulate-punctate, sometimes with one or two meandering fine rugulae. Petiole and postpetiole dorsa densely shagreened or finely and densely reticulate-punctate, usually without rugular sculpture. First gastral tergite densely punctate or shagreened, at least basally, the sculpture tending to fade out or be diminished posteriorly. Hairs on dorsum of head and alitrunk short and squat, fairly numerous but small and inconspicuous, none as large as the maximum diameter of the eye. First gastral tergite with widely scattered small squat hairs which are flattened and increase in width from base to apex. Colour medium brown, often with the gaster darker.

To the present this species is known only from Zimbabwe. Like the other members of the *arnoldi*-group it has relatively large eyes, narrow hairs in the first pronotal row (narrower than maximum eye diameter) and flattened gastral hairs which lack a long tapering basal stem. It is separated from the rest of the group by the presence of thick hairs closest to the apex of the clypeal fork; in the remaining members the apicalmost hair is elongate and fine on each tine of the fork.

MATERIAL EXAMINED

Rhodesia: Bulwayo, Hillside (*G. Arnold*); Sawmills (*G. Arnold*).

Calyptomyrmex foreli Emery

(Fig. 32)

Dicroaspis emeryi Forel, 1910*b*: 262. Syntype workers, ETHIOPIA: Eritrea, Ghinda (*K. Escherich*) (MHN, Geneva) [examined]. [Junior secondary homonym of *Calyptomyrmex emeryi* Forel, 1901: 51.]

Calyptomyrmex (*Dicroaspis*) *foreli* Emery, 1915: 15. [Replacement name for *Calyptomyrmex emeryi* (Forel). 1910.]

Calyptomyrmex (*Dicroaspis*) *pusillus* Santschi, 1915: 256. Holotype worker, GABON (*F. Faure*) (NM, Basle) [examined]. **Syn. n.**

Calyptomyrmex arnoldi subsp. *hartwigi* Arnold, 1948: 220. Syntype worker and male, SOUTH AFRICA: Pretoria, 23.i.1946 (*E. K. Hartwig*) (NM, Bulawayo) [examined]. **Syn. n.**

WORKER. TL 2·3–3·0, HL 0·58–0·68, HW 0·56–0·66, CI 95–100, SL 0·34–0·40, SI 58–61, PW 0·40–0·50, AL 0·58–0·76 (8 measured).

Mandibles usually unsculptured, smooth with scattered pits, rarely with vestigial striation which is very faint and only visible under correct lighting and at certain angles, and then is generally only visible near the base. Erect hair closest to apex on outer margins of clypeal fork elongate and fine, similar in structure to the long hairs which project forward from the vertical face of the clypeus below the fork, but shorter. Outer margin of clypeal fork behind the apicalmost hair with a second erect hair which is shorter and much stouter, contrasting strongly with the apicalmost. Eyes relatively large, maximum diameter 0·08–0·10 (0·14–0·16 × HW), much greater than the width of the hairs in the first transverse pronotal row and with >10 ommatidia. Propodeum in profile armed with a pair of angular prominences or minute denticles, without strong teeth. Metapleural lobes deep but low, with an inconspicuous thin-spot. Petiole and postpetiole both broader than long in dorsal view, the latter slightly broader than the former. Dorsum of head finely longitudinally rugulose, the rugulae diverging towards the occipital corners and the roughly triangular space between them and the occipital margin predominantly or entirely transversely rugulose. Promesonotal dorsum irregularly reticulate-rugulose, the spaces between rugulae both here and on the head finely punctulate. Dorsum of propodeum reticulate-punctate. Pedicel segments reticulate-punctate, sometimes with one or two overlying feeble rugulae. Base of first gastral tergite reticulate-punctate or densely shagreened, the sculpture usually becoming weaker posteriorly on the sclerite. Flattened hairs on promesonotal dorsum broader than those on head and more distinctly squamate. Hairs on first gastral tergite squamate, roughly tear-drop-shaped in dorsal view and without a narrow elongate stem, but visibly longer than broad. A few very fine appressed pubescent hairs present, scattered between the bizarre pilosity. Colour uniform medium to dark brown.

The main diagnostic feature of *foreli* within the group (and in the genus as a whole) is the presence of the roughly triangular area of the vertex which has transverse sculpture. Other than this *foreli* is distinguished from *stellatus* by the unique fringed pilosity of the latter, from *arnoldi* by the presence of a thick hair apicalmost on the clypeal fork and the smaller gastral hairs of that species (compare Figs 30, 32). *C. nedjem* is close to *foreli* but lacks the characteristic sculpture on the vertex and has smaller eyes. Finally, in *nummuliticus* the mandibles are sharply longitudinally striate and it has large appressed scale-like hairs on the first gastral tergite, the width of each of these hairs being equal to or greater than the distance between adjacent hairs. In *foreli* and other members of the group the width of each gastral hair is decidedly less than the distance between the hair and the ones on each side of it.

The known distribution of this obviously uncommon species is disturbing. To the present the only localities of *foreli* are those given above, namely localities in Gabon, Ethiopia and South Africa. It is most likely that the species is widely distributed in Africa but rare, but the possibility that it has been transported by man cannot be ruled out.

Calyptomyrmex nedjem sp. n.

Holotype worker. TL 2·7, HL 0·72, HW 0·70, CI 97, SL 0·44, SI 61, PW 0·48, AL 0·74.

Mandibles smooth with scattered pits, not evenly longitundinally striate but with feeble vestiges of striate sculpture basally. Hair closest to apex on outer margin of clypeal fork simple and fine, similar in appearance to the long hairs which project from the vertical face of the clypeus below the fork, but shorter. Behind the apicalmost hair others on the dorsum of the clypeal fork are shorter and much stouter, contrasting strongly with the apicalmost hair. Maximum diameter of eye 0·08 (0·11 × HW), much broader than the flattened hairs in the first pronotal row and with > 10 ommatidia. Propodeum in profile with a denticle at the point where the sloping dorsum meets the declivity. Nodes of petiole and postpetiole of approximately equal length, the node of the latter slightly broader than that of the former. Dorsum of head finely longitudinally rugulose, with a loose reticulum occipitally. Spaces between the rugulae filled with a fine dense punctulate ground-sculpture. Dorsal promesonotum densely and finely, predominantly longitudinally, rugulose but with a few irregular transverse rugulae present. Propodeal dorsum reticulate-punctate, without rugular sculpture. Dorsal surfaces of petiole and postpetiole reticulate-punctate. Base of first gastral tergite finely and superficially punctulate but this sculpture fading out posteriorly and leaving the surface weakly superficially shagreened. Small squamate scale-like hairs present on all dorsal surfaces of the head and body except the propodeum, those on the promesonotum arranged in 5 transverse rows. On the first gastral tergite the scale-like hairs are distinctly longer than broad and the spaces between adjacent hairs is greater than the widths of the individual hairs. Colour uniform medium brown.

Paratype workers. TL 2·6–2·7, HL 0·68–0·70, HW 0·68–0·70, CI 99–100, SL 0·42–0·44, SI 60–62, PW 0·44–0·48, AL 0·68–0·74 (4 measured).

As holotype but maximum diameter of eye 0.08–0.09 (0.11–0.12 × HW). Hairs on promesonotal dorsum in 5 or 6 transverse rows. Propodeum sometimes with a couple of very feeble rugulae superimposed upon the reticulate-punctate sculpture.

Holotype worker, **Zimbabwe:** Bulawayo, 5.ii.1913 (*G. Arnold*) (BMNH).

Paratypes. **Zimbabwe:** 3 workers with same data as holotype; and 1 worker, Bulawayo, 14.ii.1914 (*G. Arnold*). (BMNH; NM, Bulawayo; MCZ, Cambridge.)

After *stellatus* with its unmistakable pilosity and *arnoldi* with its thick apicalmost hair on the clypeal fork have been removed from the group, three species remain, namely *foreli, nedjem* and *nummuliticus*. The first two of these are more closely related to each other than either is to *nummuliticus*. This last-named species is large (see measurements), darkly coloured, with abundant large squamate hairs and densely striate mandibles. *C. foreli* and *nedjem* are smaller, lighter in colour, have more scattered smaller hairs and smooth (or nearly smooth) mandibles. In *foreli* the vertex of the head has a triangular area of transverse sculpture which is absent in *nedjem* and this serves to separate the two.

Calyptomyrmex nummuliticus Santschi

(Figs 29, 34)

Calyptomyrmex nummulitica Santschi, 1914*b*: 352. Syntype workers, Cameroun: Victoria (*F. Silvestri*) (NM, Basle) [examined].

Calyptomyrmex (*Calyptomyrmex*) *reticulatus* Weber, 1952: 25, fig. 17. Holotype worker, Zaire: Ituri Forest, Beni-Irumu, 17 miles [= 27km] N. of Beni, 24.ii.1948, no. 2124-1 (*N. A. Weber*) (AMNH, New York) [examined]. **Syn. n.**

Worker. TL 3·0–3·7, HL 0·76–0·92, HW 0·78–0·98, CI 102–107, SL 0·40–0·52, SI 51–56, PW 0·54–0·68, AL 0·74–0·94 (20 measured).

Mandibles usually sharply finely longitudinally densely striate, rarely the striation less conspicuous. Hair closest to apex on outer margin of clypeal fork fine and simple, situated almost at the apex, similar in appearance to the fine hairs projecting from the vertical face of the clypeus below the fork, but shorter. Hairs on the clypeal fork behind the apicalmost much thicker and contrasting strongly with it. Maximum diameter of eye 0·07–0·11 (0·09–0·12 × HW), greater than the width of the hairs in the first pronotal row. Propodeum usually armed with a pair of broad teeth where the sloping dorsum meets the declivity. These teeth are variable in size and in small specimens may be reduced to a pair of rounded prominences. Nodes of petiole and postpetiole in dorsal view of approximately equal size, or the postpetiole marginally larger. Anterior portion of dorsum of head finely and quite densely irregularly longitudinally rugulose. On the vertex this sculpture becomes a rugoreticulum which occupies at least the posterior half of the vertex and all the occipital area, but which is variable in extent, extending further forwards in some specimens than in others. Promesonotal dorsum with a strong rugoreticulum; here as on the head each reticular mesh encloses a squamate hair. Ground-sculpture on head and alitrunk a fine granulation, the surfaces matt and dull. Propodeal dorsum finely granular and dull, with weak irregular rugulae over some or all of the surface. Petiole and postpetiole nodes finely rugulose, again with dense granular ground-sculpture. First gastral tergite usually shagreened everywhere but in some this is superficial. All dorsal surfaces of head and body except the propodeum with abundant large, squamate, scale-like hairs which are much lighter (off-white to yellowish) than the underlying cuticle and hence are very conspicuous indeed. On the first gastral tergite the scale-like hairs are large and numerous, often almost as broad as long, the width of each hair usually as great as or greater than the distance separating it from adjacent hairs. Colour dark brown to blackish brown, the gaster usually lighter in shade and with a dull reddish tint.

One of the larger and more conspicuous species of African *Calyptomyrmex, nummuliticus* is easily recognized by its size, dark colour and abundant conspicuous large scale-like hairs, each of which is set in its own reticular mesh on the promesonotum and occiput.

The species is widely distributed in the forests of west and central Africa, nesting in rotten wood or in soil beneath fallen timber. Workers forage singly in the leaf litter.

MATERIAL EXAMINED

Ivory Coast: Sangrobo, S-P. de Tiassalé (*W. L. Brown & D. E. Brown*); Divo (*L. Brader*). **Ghana:** Tafo (*D. Leston*); Tafo (*B. Bolton*); Mt Atewa (*D. Leston*); Mt Atewa (*B. Bolton*); Mampong (*P. Room*). **Nigeria:** Gambari (*B. Bolton*).

Calyptomyrmex stellatus Santschi

Calyptomyrmex stellatus Santschi, 1915: 255, fig. 5. Holotype worker, GABON (*F. Faure*) (NM, Basle) [examined].

WORKER. TL 2·8, HL 0·72, HW 0·71, CI 99, SL 0·44, SI 62, PW 0·48, AL 0·72.

Mandibles finely superficially longitudinally striate. Anteriormost hair on outer margin of clypeal fork short, stout, similar to the bizarre hairs which cover the dorsum of the head and contrasting strongly with the elongate fine hairs which arise from the vertical face of the clypeus below the fork. Hairs on clypeal fork behind the apicalmost bizarre, as described below. Maximum diameter of eye 0·06 (0·08 × HW). Propodeum in profile apparently with a low rounded angle where the sloping dorsum meets the declivity. (The alitrunk is badly crushed and the shape of the propodeum difficult to discern, but it is possible to tell that propodeal teeth are absent.) Postpetiole in dorsal view larger than the petiole node, being both broader and longer. Dorsum of head with very fine, scattered irregular rugulae, the spaces between them finely punctulate or granular. Dorsal surfaces of alitrunk, petiole and postpetiole finely and densely reticulate-punctulate, the promesonotum also with a few vestigial rugulae. Base of first gastral tergite with some fine, scattered and very superficial punctulation. Bizarre hairs on head, promesonotum, pedicel segments and gaster dense, unique in form and highly characteristic. Each hair is scale-like, with a short basal stem, and the outer margins of the flattened hairs have 15–20 short, freely projecting filaments so that the margins have a fringed or ray-like appearance. Santschi described these hairs as stellate but in dorsal view they really have more the appearance of a short-tentacled sea-anemone seen from above.

Known only from the holotype worker this species is immediately diagnosed by its unique pilosity, which separates it from all other members of the genus.

The *brunneus*-group

(Figs 31, 35, 37, 38, 40–43)

First gastral tergite with the hairs elongate-clavate, elongate-spatulate or Indian club-shaped, always with a long narrow or tapering basal stem. Maximum diameter of eye always greater than the width of the hairs in the first transverse pronotal row.

The seven species of this group (*brunneus, clavatus, clavisetus, duhun, rennefer, shasu, tensus*) are widely distributed in the Ethiopian region although most are only known from one or two localities. To the present all the species in this group are known to have a distribution in eastern, central and southern Africa; none have yet been found in West Africa although those occurring in Zaire or Uganda may well be present there. In summary *clavisetus* and *brunneus* occur in South Africa (the latter also being known from Zimbabwe), whilst the rest are more northerly, with *clavatus* from Ethiopia, Zaire and Kenya, *rennefer* from Zaire, *tensus* from Uganda, *duhun* from Uganda, Kenya and Zaire, and *shasu* from Uganda, Tanzania, Burundi and Zaire.

Of the seven species *tensus* is the only one in which the apicalmost hair on the clypeal fork is stout and thick, and *shasu* is the sole species where bizarre hairs similar to those on the first gastral tergite occur all over the first sternite also. In all other species such hairs are restricted to the apical portion of the sternite or are lacking on the sclerite. Of the remainder *rennefer* has very long body hairs which are only feebly clavate apically, and also has all hairs on the clypeal fork simple. In *duhun* the propodeum is strongly transversely sculptured, a feature lacking in *brunneus, clavisetus, clavatus* and the previously mentioned members of this group.

The last three species mentioned form a closely related complex, with *brunneus* being darkly coloured and the other two light brown. Finally, in *clavatus* the petiole and postpetiole nodes are of approximately equal size, while in *clavisetus* the postpetiole is much larger.

Calyptomyrmex brunneus Arnold

Calyptomyrmex brunneus Arnold , 1948: 221. Holotype worker, SOUTH AFRICA: Transvaal, Ngomi Forest, 21.ii.1946 (*J. C. Faure*) (NM, Bulawayo) [examined].

WORKER. TL 2·6–2·7, HL 0·68–0·70, HW 0·64–0·66, CI 94–97, SL 0·42–0·44, SI 65–67, PW 0·48–0·50, AL 0·72–0·74 (5 measured).

Mandibles varying from superficially finely marked without definite sculpture to finely and very delicately striate. Clypeal fork in dorsal view with fairly long prongs, the outer margins of which are shallowly convex, not strongly bowed outwards and caliper-like. Hair closest to apex of clypeal fork on outer margin fine, similar in structure to those which arise from the vertical face of the clypeus below the fork, but shorter. Hairs on the clypeal fork behind the apicalmost much thicker and contrasting with it. Maximum diameter of eye 0.07–0.08 (0.11–0.13 × HW), much greater than the maximum widths of the hairs in the first pronotal row and at most with about 15 ommatidia. Propodeum in profile armed with a pair of denticles or short teeth where the sloping dorsum meets the declivity. With the pedicel segments in dorsal view the postpetiole distinctly larger than the petiole, markedly broader and also longer. Dorsum of head finely, sharply and quite densely irregularly longitudinally rugulose, with conspicuous dense punctulate ground-sculpture between the rugulae. Promesonotum finely rugulose and with ground-sculpture as on the head. The rugulae on the promesonotum are usually irregular but in some are predominantly longitudinal. Dorsal surfaces of propodeum, petiole and postpetiole densely reticulate-punctate. Base of first gastral tergite superficially punctulate or shagreened, this usually fading out more posteriorly on the sclerite or at least becoming weaker. All dorsal surfaces of head and body except the propodeum with numerous conspicuous clavate or Indian club-shaped hairs. Colour uniform dark brown to blackish brown, the pale hairs rendered more obvious by the dark colour of the cuticle.

C. brunneus is most closely related to *clavatus* and *clavisetus*. Differences between these species, and between them and other members of the group, are discussed under the last two names mentioned.

MATERIAL EXAMINED
Zimbabwe: Vumba Mts (*G. Arnold*).

Calyptomyrmex clavatus Weber

(Fig. 41)

Calyptomyrmex (*Calyptomyrmex*) *clavatus* Weber, 1952 23, figs 20, 22, 24. Holotype worker, KENYA: 1°25′S 35°10′W [sic], to 1°38′S, 35°17′E, 27.i.1948, no. 2000 (*N. A. Weber*) (AMNH, New York) [examined].

WORKER. TL 2·7–2·9, HL 0·64–0·68, HW 0·62–0·66, CI 96–97, SL 0·38–0·40, SI 60–61, PW 0·46–0·48, AL 0·68–0·74 (3 measured).

Mandibles unsculptured or at most with faint superficial markings, not longitudinally striate. Hair closest to apex on outer margin of clypeal fork fine, similar in appearance to the fine hairs which project from the face of the clypeus below the fork, but shorter. Others hairs on clypeal fork behind the apicalmost thick, contrasting with it. Maximum diameter of eye 0·07–0·08 (0·11–0·12 × HW), much greater than the widths of the hairs in the first pronotal row, with 18 to >20 ommatidia. Propodeum armed with a pair of denticles. Petiole and postpetiole in dorsal view of approximately equal size, the postpetiole marginally broader than the petiole. Dorsum of head finely and densely longitudinally rugulose, the rugulae diverging away from the mid-line towards the occipital corners. Ground-sculpture of head a fine and quite dense punctulation. Promesonotal dorsum finely and irregularly rugulose, reticulate in places, and with dense punctulate ground-sculpture. Propodeal dorsum, petiole and postpetiole densely reticulate-punctate. First gastral tergite finely punctulate basally, this sculpture becoming reduced more posteriorly on the sclerite. All dorsal surfaces of head and body except for propodeum with numerous clavate or Indian club-shaped hairs which are relatively short; those on the first gastral tergite shorter than the maximum diameter of the eye. Colour uniform medium brown.

Within the *brunneus*-group *clavatus* is most closely related to *clavisetus* but the two are separated by the fact that the postpetiole in *clavisetus* in dorsal view is much larger than the petiole, whereas in *clavatus* they are approximately the same size. Another closely related species is *brunneus,* but here again the postpetiole is obviously broader than the petiole and the body is much darker brown or blackish brown in colour.

Other species with elongate-clavate or Indian club-shaped hairs are easily separated from *clavatus,* as in *tensus* the apicalmost hair on the clypeal fork is thick (fine in *clavatus*), in *shasu* the first gastral sternite has bizarre pilosity like that on the tergite (not so in *clavatus*), in *duhun* the propodeum is coarsely transversely rugose (punctate in *clavatus*), and in *rennefer* the clavate hairs are very long and narrow, those on the gaster exceeding the maximum diameter of the eye.

MATERIAL EXAMINED

Ethiopia: Harrar (no collector's name but probably *Escherich*). **Zaire:** Yangambi (*M. Maldague*).

Calyptomyrmex clavisetus (Santschi)

(Fig. 42)

Dicroaspis claviseta Santschi, 1914*a*: 27. Syntype workers, SOUTH AFRICA: Natal, Pietermaritzburg, 21.iii. 1905 (*I. Trägårdh*) (NM, Basle) [examined].

Calyptomyrmex (*Dicroaspis*) *clavisetus* (Santschi) Emery, 1915: 15 [implied in text].

WORKER. TL 2·1–2·6, HL 0·56–0·64, HW 0·52–0·60, CI 93–94, SL 0·34–0·36, SI 60–65, PW 0·34–0·42, AL 0·58–·66 (4 measured).

Mandibles smooth with the faintest traces of superficial markings, not longitudinally striate. Clypeal fork short and caliper-like, the outer edges of the prongs of the fork strongly bowed outwards. Hair closest to apex on outer margin of clypeal fork fine, similar in appearance to the long hairs which project from the vertical face of the clypeus below the fork. Hairs on the fork behind the apicalmost much stouter and contrasting with the apicalmost. Maximum diameter of eye 0·06–0·07 (0·12 × HW), much greater than the maximum width of the hairs in the first transverse pronotal row and with 15 or fewer ommatidia. Propodeum armed with a pair of denticles or short teeth where the sloping dorsum of the propodeum meets the declivity. Postpetiole in dorsal view distinctly more massive than petiole node, both broader and longer than it. Dorsum of head finely and quite densely irregularly longitudinally rugulose, the individual rugulae narrow but quite sharp and well-defined. Spaces between rugulae with a fine, dense and very conspicuous reticulate-punctate ground-sculpture. Promesonotal dorsum irregularly rugulose and with dense reticulate-punctate ground-sculpture. Dorsal surfaces of propodeum, petiole and postpetiole densely reticulate-punctate, without rugular sculpture or at most with very faint vestiges on the propodeum. Base of first gastral tergite superficially faintly shagreened, this sculpture fading out posteriorly on the sclerite. All dorsal surfaces of head and body except the propodeum with numerous clavate or Indian club-shaped hairs. Colour uniform light brown to medium brown.

Three small species of this group, *brunneus, clavatus* and *clavisetus,* are closely related and taken together they can be separated from all other members by the following differentiating characters being present together in a single specimen. Firstly, the apicalmost clypeal fork hair is fine but others on the fork are stout. Secondly, the propodeum lacks transverse rugae. Thirdly, the first gastral sternite does not have hairs like those on the tergite all over the surface; any which are present are restricted to the posterior one-third of the sternite. Finally, the clavate or Indian club-shaped hairs are not exceptionally long and fine on the first gastral tergite.

Within these limits *clavatus* is distinguished from the other two by having larger eyes and pedicel segments which in dorsal view are of approximately equal size, the postpetiole not being noticeably larger than the petiole. In both *brunneus* and *clavisetus* the eyes are smaller and the postpetiole is markedly larger than the petiole in dorsal view. These last two are separated on size (*brunneus* being larger) and by the shape of the clypeal fork, which in *brunneus* is longer and has straighter sides, whilst in *clavisetus* it is very short and has strongly bowed outer margins.

MATERIAL EXAMINED

South Africa: Natal, Umhlanga (*G. Arnold*).

Calyptomyrmex duhun sp. n.

(Fig. 37, 43)

HOLOTYPE WORKER. TL 3·3, HL 0·78, HW 0·76, CI 97, SL 0·48, SI 63, PW 0·54, AL 0·88

Mandibles finely superficially striate. Hair closest to apex on outer margin of clypeal fork elongate and fine, similar in appearance to those projecting from the vertical face of the clypeus below the fork, but shorter. Hairs on clypeal fork behind the apicalmost short and very much stouter, contrasting strongly with it. Maximum diameter of eye 0·08 (0·11 × HW), much greater than the width of the hairs in the first transverse pronotal row and with > 10 ommatidia. Propodeum in profile with a pair of triangular teeth. Dorsum of head finely and densely irregularly longitudinally rugulose, grading into a loose irregular and broken ruguloreticulum occipitally. Spaces between rugulae with a densely punctulate ground-sculpture. Promesonotal dorsum densely, closely and coarsely irregularly rugulose. Propodeal dorsum transversely concave and conspicuously transversely strongly rugulose, without punctate ground-sculpture. Petiole and postpetiole feebly rugulose dorsally and with weak punctulate to granular ground-sculpture. First gastral tergite with fine superficial shagreening. All dorsal surfaces of head and body except for propodeum with numerous flattened clavate or Indian club-shaped hairs, very conspicuous on the first gastral tergite. Colour dark brown, the gaster with a reddish tint and somewhat lighter.

PARATYPE WORKERS. TL 3·2–3·6, HL 0·78–0·84, HW 0·76–0·82, CI 97–98, SL 0·47–0·51, SI 62–63, PW 0·52–0·60, AL 0·88–0·96 (2 measured).

As holotype but propodeal teeth of variable size. Maximum diameter of eye 0·08–0·10 (0·10–0·12 × HW).

Holotype worker, **Uganda:** Ft Portal, ii.1948, no. 2095 (*N. A. Weber*) (MCZ, Cambridge).

Paratypes. **Zaire** (='B. Congo' on data label): 1 worker, W. side Ruwenzori, ii.1948, no. 2112 (*N. A. Weber*). **Kenya:** 1 worker, Kaimosi Mission, 27 miles (= 43.4 km) NE. of Kisumu, 1650 m, 29.xi.1957 (*E. S. Ross & R. E. Leech*) (MCZ, Cambridge; BMNH).

This is the only member of the *brunneus*-group which has transverse rugose sculpture on the propodeal dorsum. All other species show a fairly conspicuous reticulate-punctate sculpture and, although a few may have some feeble rugulae, these are usually not transverse and are always inconspicuous. Apart from this, *tensus* has a thick apicalmost hair on the clypeal fork, *shasu* has bizarre hairs all over the first gastral sternite, *rennefer* has all clypeal fork hairs simple and also has long narrow body pilosity. The species related to *brunneus* (*clavatus, clavisetus*) are smaller and for the most part have the mandibles unsculptured.

Calyptomyrmex rennefer sp. n.

(Fig. 35)

HOLOTYPE WORKER. TL 2·9, HL 0·72, HW 0·74, CI 103, SL 0·44, SI 59, PW 0·52, AL 0·80.

Mandibles with fine sculpture basally but this fades out towards the apical (masticatory) margin, leaving a smooth strip. Hair closest to apex on outer margin of clypeal fork, and all other hairs on the clypeal fork, simple, similar in appearance to the elongate hairs which project from the vertical face of the clypeus below the fork, but shorter. Maximum diameter of eye 0·06 (0·08 × HW), distinctly much greater than the width of the hairs in the first transverse pronotal row and with 10–11 ommatidia. Propodeum in profile armed with a pair of triangular denticles. Petiole node in profile larger than that of postpetiole, in dorsal view the latter slightly broader than the former. Head in dorsal view finely irregularly and quite densely longitudinally rugulose, the rugulae arising on or just behind the frontal lobes, roughly paralleling the line of the scrobe margin and directed towards the occipital corner. Occipital region of head with some scattered cross-meshes but without a developed reticulum. Spaces between rugulae packed with a fine and very dense reticulate-punctate ground-sculpture, the dorsal surfaces of many of the rugulae with a beaded appearance due to the presence of aligned punctulae upon them. Promesonotal dorsum densely and quite coarsely rugulose, predominantly longitudinally so, but with numerous scattered short cross-meshes. Ground-sculpture as on head but less conspicuous because the rugulae on the promesonotal dorsum are more tightly packed than on the head. Propodeal dorsum densely and strongly reticulate-punctate, without rugulose sculpture. Petiole and postpetiole dorsally predominantly reticulate-punctulate and with sparse fine rugulae also present. First gastral tergite very lightly superficially reticulate or reticulate-punctulate everywhere. Hairs present and numerous on all dorsal surfaces of the head and body except the propodeum, characteristically shaped, elongate and fine but narrowly clavate apically; those on the first gastral tergite distinctly much longer than the maximum diameter of the eye. Colour uniform dark brown.

PARATYPE WORKERS. TL 2·8–3·0, HL 0·70–0·74, HW 0·72–0·76, CI 100–104, SL 0·40–0·44, SI 54–59, PW 0·50–0·54, AL 0·78–0·86 (8 measured).

Maximum diameter of eye 0·06 (0·08 × HW), with 10–14 ommatidia. Mandibles usually as in holotype but in some the sculpture almost completely effaced, the blade virtually smooth. A few weak rugulae, formed by the alignment of the margins of adjacent punctures, may occur on the propodeal dorsum. On the promesonotum the cross-meshes on the dorsum are sometimes almost as strongly developed as the longitudinal rugulae.

Holotype worker, **Zaire:** Kivu, Terr. Lubero, riv. Lubero, 1780 m, 10.vi.1954, coll. Mus. Congo, tamisage de terreau (*R. P. M. J. Celis*) (MRAC, Tervuren).

Paratypes, **Zaire:** 6 workers with same data as holotype; 2 workers, Kivu, Kabare Nyakasiba 2350, xii.1950, forêt de montagne, I.R.S.A.C. -Mus. Congo, récolté dans terreau, au Berlese (*N. Leleup*) (MRAC, Tervuren; BMNH; MCZ, Cambridge; NM, Basle).

An ergatoid female, housed in MRAC, Tervuren, is certainly to be associated with this species. It is extremely ergatoid, with all the characters given above, but is larger, HL 0·82, HW 0·84, AL 0·90, has much larger eyes, maximum diameter 0·14 (0·17 × HW), and has ocelli present. The data on this specimen are: Zaire, Kivu, Terr. Lubero, route Kimbulu, 1830 m (ravin), iv.1954, coll. Mus. Congo, tamisage de terreau sous fougères arbor (*R. P. M. J. Celis*).

The form of the pilosity immediately distinguishes *rennefer* from all other known African species. The long narrow hairs with feebly clavate apices are not duplicated in any other species. Coupled with this, *rennefer* is one of the very few species in which all the hairs on the clypeal fork are simple.

This species is one of two African forms in which an ergatoid female is known, the other being *piripilis*. Notes on the known females are given under the discussion of that species.

Calyptomyrmex shasu sp. n.

(Fig. 38)

HOLOTYPE WORKER. TL 3·4, HL 0·84, HW 0·78, CI 93, SL 0·52, SI 67, PW 0·52, AL 0·88.

Mandibles finely and densely longitudinally striate. Hair closest to apex on outer margin of clypeal fork simple, similar in appearance to the long hairs which project from the vertical face of the clypeus below the fork, but shorter. Other hairs on dorsum of clypeal fork stout and clavate, contrasting strongly with the apicalmost. Maximum diameter of eye 0.08 (0.10 × HW), greater than the maximum width of the hairs in the first transverse pronotal row and with about 14 ommatidia. Propodeum in profile armed with a pair of short triangular teeth. Nodes of petiole and postpetiole of approximately equal width in dorsal view, the latter only fractionally broader than the former. Dorsum of head finely and densely longitudinally rugulose, the individual rugulae narrow and somewhat divergent posteriorly. Spaces between the rugulae filled with a very conspicuous, dense reticulate-punctate ground-sculpture. Promesonotal dorsum weakly irregularly rugulose, with irregular open reticular meshes in places. Reticulate-punctate ground-sculpture superficial and much less conspicuous than on the head. Propodeal dorsum reticulate-punctate. Petiole and postpetiole reticulate-punctate dorsally, with vestiges of rugular sculpture in places. First gastral tergite only weakly sculptured, with a faint superficial reticular patterning. All dorsal surfaces of head and body except for the propodeum with a dense array of flattened, thickly clavate hairs which are very conspicuous. First gastral sternite everywhere with hairs similar to those on the tergite. Colour medium brown, varying in shade over the body.

PARATYPE WORKERS. TL 3.3–3.5, HL 0.76–0.86, HW 0.72–0.82, CI 93–95, SL 0.46–0.52, SI 63–68, PW 0.48–0.54, AL 0.80–0.90 (15 measured).

Maximum diameter of eye 0·07–0·08 (0·09–0·11 × HW), with 13–16 ommatidia. Colour varying from fairly light to dark brown. Intensity of sculpture variable, in some the promesonotal rugulae are strong and the weak ground-sculpture virtually effaced. Propodeal teeth usually short and triangular but may be very low and blunt or somewhat elongated to a short triangular point. Variation is common and the two teeth may vary in shape and size on a single specimen.

Holotype worker, **Burundi:** Bujumbura, 1977, no. 1 (*A. Dejean*) (BMNH).

Paratypes. **Burundi:** 8 workers with same data as holotype. **Tanzania:** 3 workers, Kilimanjaro, Marangu, I.R.S.A.C.-Mus. Congo, 2400 m, 20.ii.1956, Mission Zoolog. IRSAC en Afrique orientale P. Basilewsky et N. Leleup, forêt mont., humus (*J. & N. Leleup*). **Uganda:** 4 workers and 1 dealate female, E. Ruwenzori, Kalengire, 2000 m, 14.i.1954, coll. Mus. Congo, dans bois mort (*R. P. M. J. Celis*); 15 workers and 2 females (one alate), E. Ruwenzori, ruiss. Murusege, 2275 m, 25.i.1954, coll. Mus. Congo, dans terreau de bambous (*R. P. M. J. Celis*). **Zaire:** 2 workers, Kivu, Terr. Lubero, route Kimbulu, 1830 m (ravin), iv.1954, coll. Mus. Congo, tamisage de terreau sous fougères arbor (*R. P. M. J. Celis*); 2 workers, Kivu, t. lubero, rés. forest Biena, 1800 m, 24.vii.1954, coll. Mus. Congo, dans terreau, au Berlese (*R. P. M. J. Celis*); 1 worker, P.N.A., 30.i.-21.ii.1953, Massif Ruwenzori, Kalonge, 2060 m, Ruiss. Karambura affl. Kataulenko, 2225–59 (*P. Vanschuytbroeck & J. Kekenbosch*). (BMNH; MRAC, Tervuren; MCZ, Cambridge; NM, Basle; NM, Bulawayo.)

C. shasu is a very distinctive species, immediately characterized by its possession of bizarre hairs all over the first gastral sternite which are similar to those on the first tergite. This is the only known species to show this development; in all others the sternite either lacks hairs similar to those on the tergite or has them restricted to the posterior one-third of the sclerite.

Calyptomyrmex tensus **sp. n.**

(Figs 31, 40)

HOLOTYPE WORKER. TL 2·5, HL 0·62, HW 0·59, CI 95, SL 0·35, SI 59, PW 0·41, AL 0·64.

Mandibles mostly smooth and shining, with only the faintest vestiges of sculpture in places. Hair closest to apex on outer margin of clypeal fork stout, contrasting with the long fine hairs which project from the face of the clypeus below the fork. Other hairs on clypeal fork behind the apicalmost also stout, similar to the apicalmost hair in construction. Maximum diameter of eye 0·06 (0·10 × HW), greater than the width of the hairs in the first transverse pronotal row and with 9–10 ommatidia. Propodeum in profile armed with a pair of very low but quite broadly triangular denticles. Metapleural lobes strongly prominent, with a conspicuous almost circular thin-spot. Petiole node in profile higher than that of postpetiole. In dorsal view the postpetiole node marginally broader than that of the petiole. Dorsum of head extremely finely longitudinally rugulose, the rugulae for the most part scarcely stronger than the underlying dense reticulate-punctulate ground-sculpture. Promesonotal dorsum finely irregularly rugulose, the rugulae stronger than on the head and forming a loose, open-meshed reticulum on the pronotum. Ground-sculpture finely reticulate-punctulate. Propodeal dorsum densely reticulate-punctate, with a few weak rugulae formed by alignment of the walls of the punctures. Petiole and postpetiole densely reticulate-punctulate with a few very feeble rugular vestiges. Base of first gastral tergite superficially punctulate to shagreened, fading out posteriorly. All dorsal surfaces of head and body except for propodeum densely clothed with elongate-spatulate hairs. In dorsal view those on the first gastral tergite much longer than broad and gradually increasing in width from the narrow base to the blunt apex. Colour uniform mid-brown.

Holotype worker, **Uganda:** Ruwenzori Expd., nr Mubuku Rr, c. 1 mile [1.61 km] SE. Ibanda, 30.vii.1952, no. 128, soil and litter under elephant grass (*G. O. Evans*) (BMNH).

This small species, known only from the holotype, is one of five African forms in which the apicalmost hair on the clypeal fork is stout. The other four are *stellatus, brevis, piripilis* and *arnoldi*. The first of these is isolated from *tensus* by its truly unique pilosity (see description), the next two by their possession of very small eyes which are smaller in diameter than the widths of the hairs in the first pronotal row, and the last named separates from *tensus* on the shape of the bizarre hairs on the first gastral tergite. In *arnoldi* these hairs are short, squat and widely scattered whilst in *tensus* they are longer, narrower and denser (compare Figs 30, 31). *C. tensus* is quickly separated from other members of the *brunneus*-group as it is the only species within the group bearing a stout apicalmost hair on the clypeal fork.

Acknowledgements

I would like to express my thanks and gratitude to the following for their unstinting assistance in tracking down the types and other material which was used in this study.

Dr Claude Besuchet (MHN, Geneva); Mrs Cathy Car (NM, Bulawayo); Dr Jean Decelle (MRAC, Tervuren); Mrs Marjorie Favreau (AMNH New York); Professor Egidio Mellini (IE, Bologna); Dr Roberto Poggi (MCSN, Genoa); Mrs Margaret Thayer (MCZ, Cambridge); Dr Cesare Baroni Urbani (NM, Basle); and Mme J. Casevitz Weulersse (MNHN, Paris).

Finally, I am grateful to Mr David Morgan who drew the excellent Figs 26 and 27.

References

André, E. 1884. *In* Magretti, P., Risultati di raccolte imenotterologiche nell'Africa orientale. *Annali Mus. civ. Stor. nat. Genova* **21:** 523–636, 1 pl.

—— 1892. Matériaux myrmécologiques. *Revue Ent.* **11:** 45–56.

Arnold, G. 1914. Nest-changing migrations in two species of ants. *Proc. Rhod. scient. Ass.* **13:** 25–32, 1 pl.

—— 1917. A monograph of the Formicidae of South Africa, part 3. *Ann. S. Afr. Mus.* **14:** 271–402.

——1926. A monograph of the Formicidae of South Africa, appendix. *Ann. S. Afr. Mus.* **23:** 191–295, figs 60–82.

—— 1948. New species of African Hymenoptera, no. 8. *Occ. Pap. nat. Mus. sth. Rhod.* **14:** 213–250, 23 figs.

Bernard, F. 1952. La réserve naturelle intégrale du Mt. Nimba, part 11. Hyménoptères Formicidae. *Mém Inst. fr. Afr. noire* **19:** 165–270, 3 pls., 15 figs.

Bingham, C. T. 1903. *Fauna of British India, including Ceylon and Burma.* Hymenoptera **2,** Ants and Cuckoo Wasps. 506 pp., 161 figs, 1 pl. London.

Bolton, B. 1973 A remarkable new arboreal ant genus from West Africa. *Entomologist's mon. Mag.* **108:** 234–237, 3 figs.

Brown, W. L. 1949. Revision of the ant tribe Dacetini, 4. Some genera properly excluded from the Dacetini, with the establishment of the Basicerotini, new tribe. *Trans. Am. ent. Soc.* **75:** 83–96.

Donisthorpe, H. St. J. K. 1948. A new genus and species of dacetine ant from New Guinea. *Entomologist's mon. Mag.* **84:** 281, fig. 1.

Emery, C. 1886. Alcune formiche africane. *Boll. Soc. ent. ital.* **18:** 355–366, pl. 17.

—— 1887. Catalogo delle formiche esistente nelle collezioni del Museo Civico di Genova. Parte terza. Formiche della regione Indo-Malese e dell' Australia. *Annali Mus. civ. Stor. nat. Genova* (2) **5:** 427–473, 2 pls.

—— 1895. Voyage de ME. Simon dans l'Afrique australe (janvier-avril 1893). Formicides. *Annls Soc. ent. Fr.* **64:** 15–56, 1 pl.

—— 1908. Descriptions d'un genre nouveau et de plusieurs formes nouvelles de fourmis du Congo. *Annls Soc. ent. Belg.* **52:** 184–189, 2 figs.

—— 1914. Intorno alla classificazione dei Myrmicinae. *Rc. Sess. Accad. Sci. Ist Bologna* **1914:** 27–42.

—— 1915. Formiche raccolte nell' Eritrea dal Prof. F. Silvestri. *Boll. Lab. Zool. gen. agr. Portici* **10:** 3–26, 13 figs.

—— 1922. Hymenoptera fam. Formicidae subfam. Myrmicinae. *In* Wytsman, P. A. G., *Genera Insect.* fasc. **174c:** 207–397, 7 pls.

Forel, A. 1901. Formiciden des Naturhistorisches Museums zu Hamburg. Neue *Calyptomyrmex-, Dacryon-, Podomyrma-* und *Echinopla-* Arten. *Mitt. naturh. Mus. Hamb.* **18:** 43–82.

—— 1907. Formicides du musée national hongrois. *Annls hist.-nat. Mus. natn. hung.* **5:** 1–42.

—— 1910*a*. Notes sur quelques fourmis d'Afrique. *Annls Soc. ent. Belg.* **54:** 421–458.

—— 1910*b*. Ameisen aus der Kolonie Erythräa. Gesammelt von Prof. Dr. K. Escherich (nebst einigen in West-Abessinien von Herrn A. Ilg gesammelten Ameisen). *Zool. Jb. Syst.* **290:** 243–274.

——1913. Fourmis de Rhodesia, etc. récoltées par MG. Arnold, le Dr H. Brauns et K. Fikendey. *Annls Soc. ent. Belg.* **57:** 108–147.

Guérin-Méneville, F.-E. 1844. *Iconographie du règne animal de G. Cuvier.* 576 pp., 104 pls. Paris.

Karavaiev, V. 1931. Ameisen aus Englisch-Ostafrika. *Zool. Anz.* **95:** 42–51, 7 figs.

Kugler, C. 1978. A comparative study of the myrmicine sting apparatus. *Studia ent.* **20**: 413–548, 244 figs.

—— 1979. Evolution of the sting apparatus in the myrmicine ants. *Evolution* **33**: 117–130, 5 figs.

Lowne, B. T. 1865. Contributions to the natural history of Australian ants. *Entomologist* **22**: 331–336.

Mayr, G. 1901. Südafrikanische Formiciden gesammelt von Dr Hans Brauns. *Annln naturh. Mus. Wien* **16**: 1–30, 2 pls.

Menozzi, C. 1924. Alcune nuove formiche africane. *Annali Mus. civ. Stor. nat. Genova* **51**: 220–227, 8 figs.

Santschi, F. 1914*a* Meddelanden från Göteborgs Musei Zoologiska Afdeling no. 3. Fourmis du Natal et du Zululand récoltées par le Dr I. Trägårdh; avec un appendice. Notes biologiques par I. Trägårdh. *Göteborgs K. Vetensk.-o. VitterhSamh. Handl.* **15**: 1–47, 10 figs.

—— 1914*b*. Formicides de l'Afrique occidentale et australe du voyage de M le Professeur F. Silvestri. *Boll. Lab. Zool. gen. agr. Portici* **8**: 308–385, 34 figs.

—— 1915. Nouvelles fourmis d'Afrique. *Annls Soc. ent. Fr.* **84**: 244–285, 15 figs.

——1919. Nouvelles fourmis du Congo Belge du Musée du Congo Belge, à Tervuren. *Revue Zool. Bot. afr.* **7**: 79–91.

—— 1923. Descriptions de nouveaux formicides éthiopiens et notes diverses 1. *Revue Zool. Bot. afr.* **11**: 259–295, 5 figs.

—— 1932. Formicides Sud-Africains. *Soc. ent. Fr. Livre du centenaire* **1932**: 381–392, 12 figs.

Smith, F. 1853. Monograph of the genus *Cryptocerus*, belonging to the group Cryptoceridae, family Myrmicidae, division Hymenoptera Heterogyna. *Trans. ent. Soc. Lond.* (2) **2**: 213–228, pls 19–21.

Urbani, C. B. 1971. Einige Homonymien in der Familie Formicidae. *Mitt. schweiz. ent. Ges.* **44**: 360–362.

—— 1975. Primi reperti del genre *Calyptomyrmex* Emery nel subcontinente Indiano. *Ent. Basiliensia* **1**: 395–411, 8 figs.

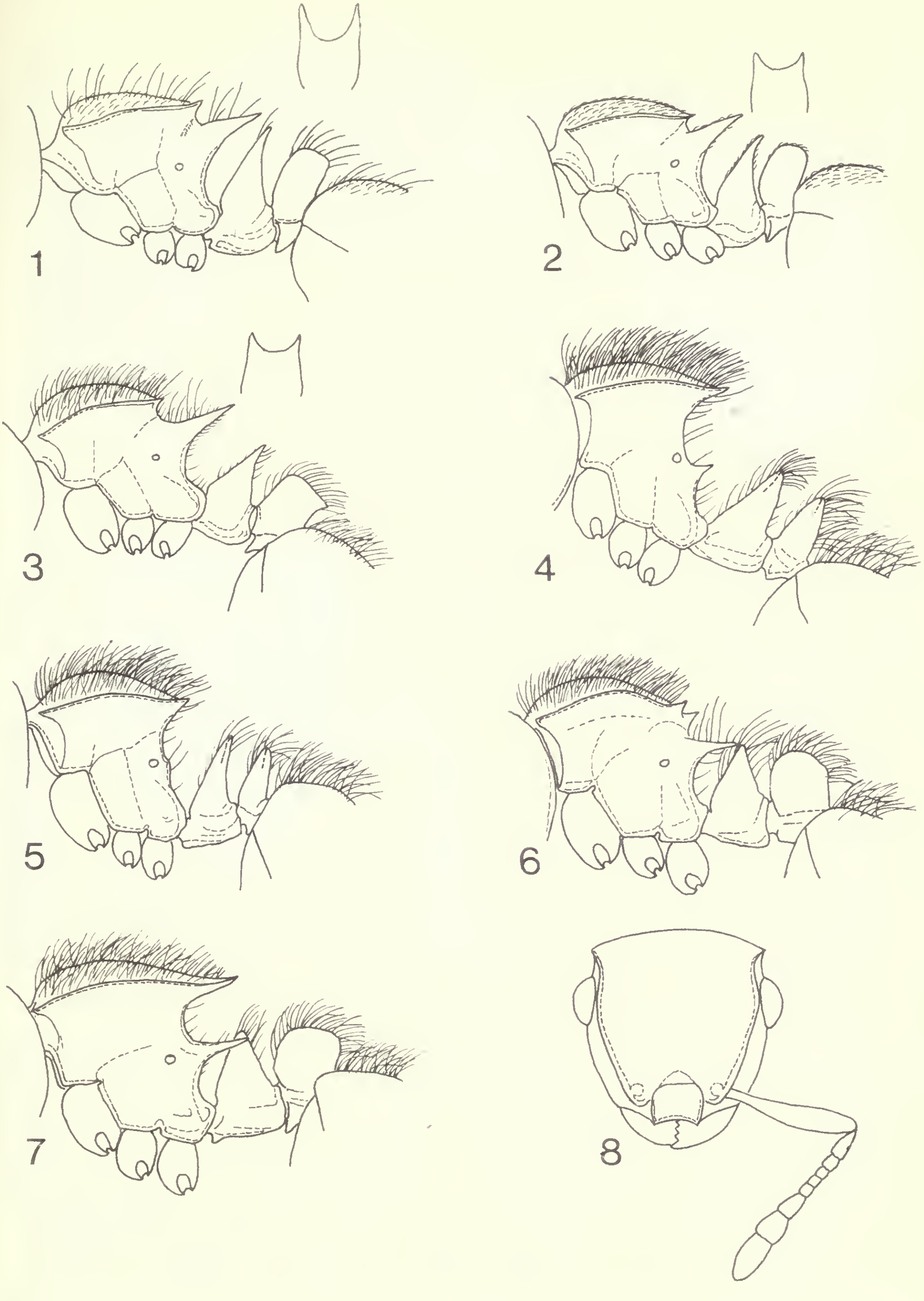
Viemeyer, H. 1922. Neue Ameisen. *Arch. Naturg.* **88** (A)7: 203–220, 2 figs.

Weber, N. A. 1943. Ants of the Imatong Mountains, Anglo-Egyptian Sudan. *Bull. Mus. comp. Zool. Harv.* **93**: 261–389, 16 pls.

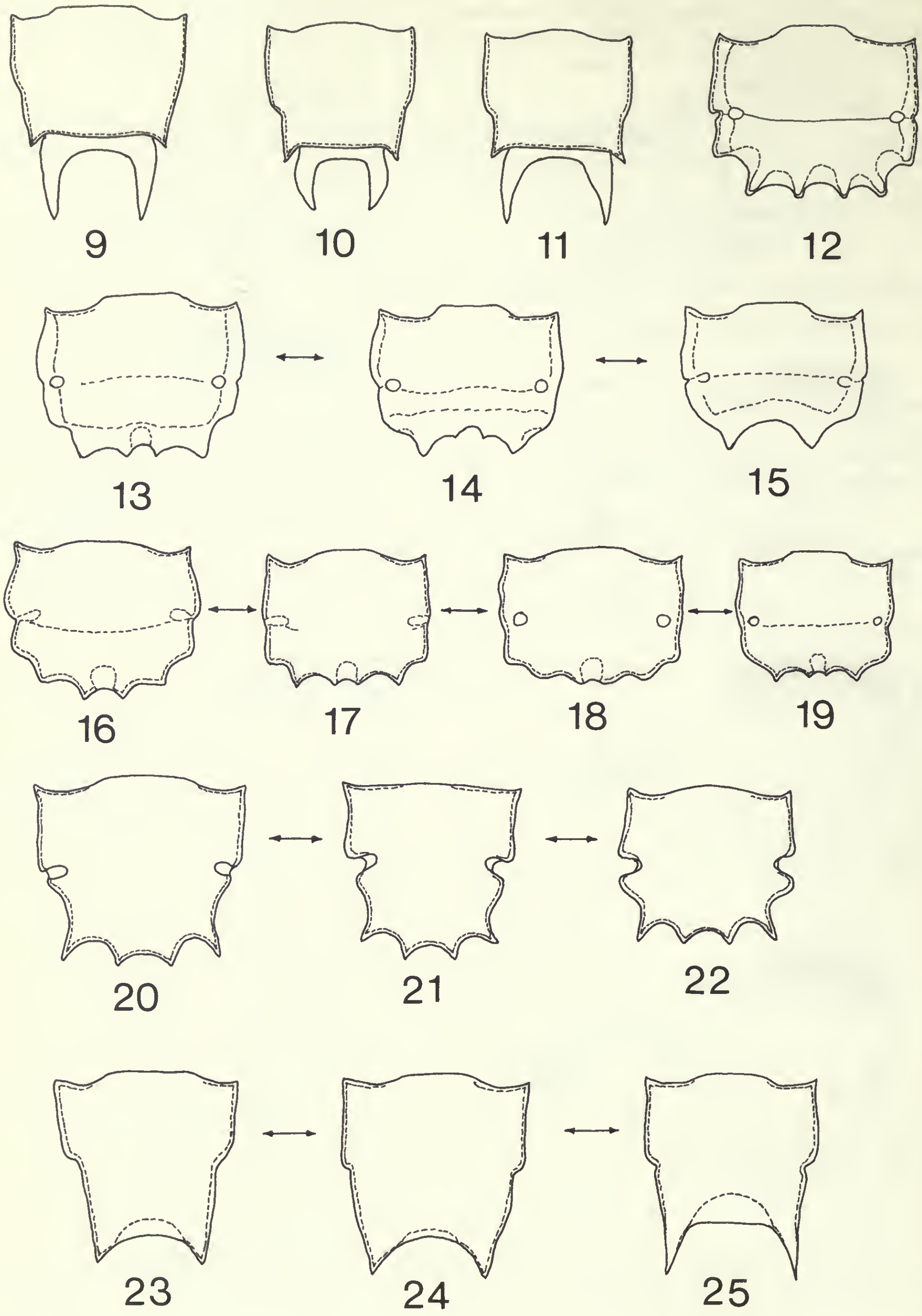
—— 1952. Studies on African Myrmicinae, 1. *Am. Mus. Novit.* no. 1548: 1–32, 36 figs.

Wheeler, W. M. 1922. Ants of the Belgian Congo, parts 1–8. *Bull. Am. Mus. nat. Hist.* **45**: 1–1139, 23 pls, 76 figs.

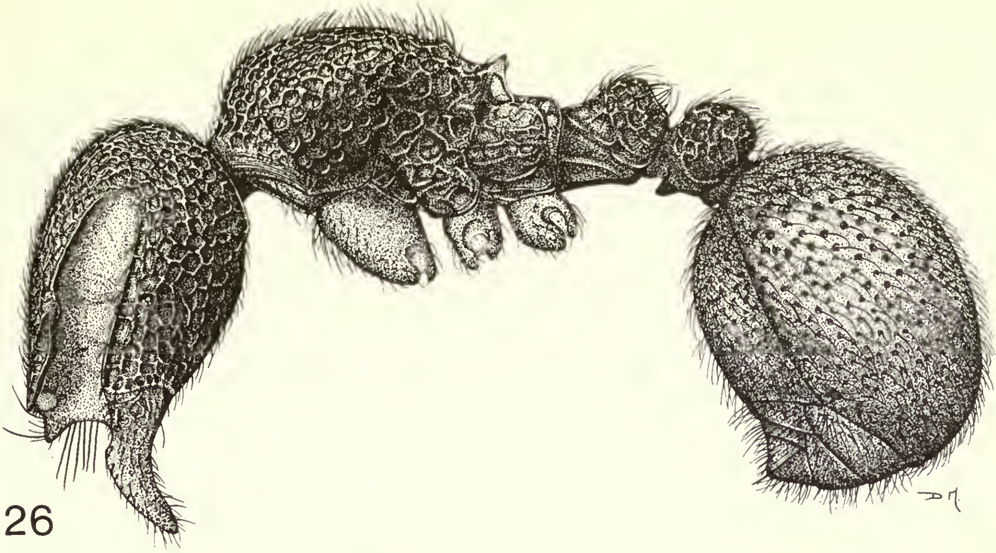
—— 1935. Two new genera of myrmicine ants from Papua and the Philippines. *Proc. New Engl. zool. Cl.* **15**: 1–9, 2 figs.

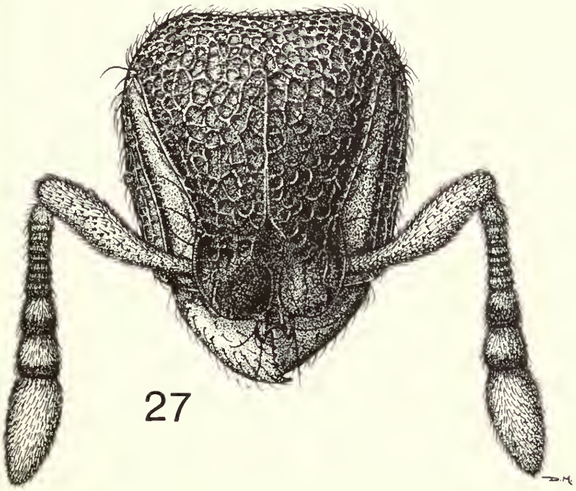


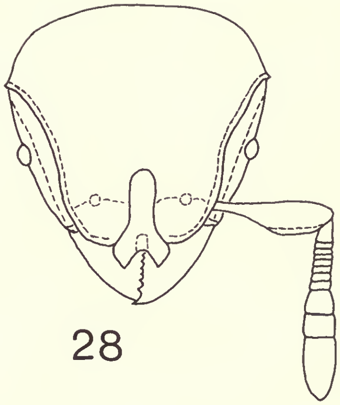
Figs 1–8 *Meranoplus* workers. 1–7. Alitrunk and pedicel segments of (1) *sthenus*, (2) *glaber*, (3) *spininodis*, offsets show petiole in anterior view, (4) *nanus*, (5) *inermis*, (6) *peringueyi*, (7) *magrettii*. *8, Head of magrettii*, pilosity omitted.

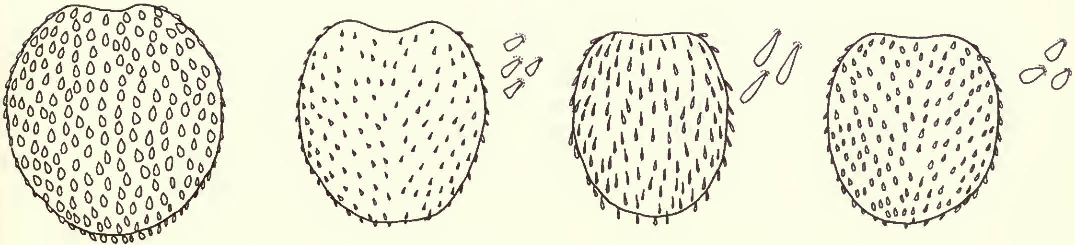

9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Figs 9–15 *Meranoplus* workers. Promesonotal shield of (9) *sthenus*, (10) *glaber*, (11) *spininodis*, (12) *nanus*, (13–15) *clypeatus*, (16–19) *inermis*, (20–22) *peringueyi*, (23–25) *magrettii*; pilosity omitted.

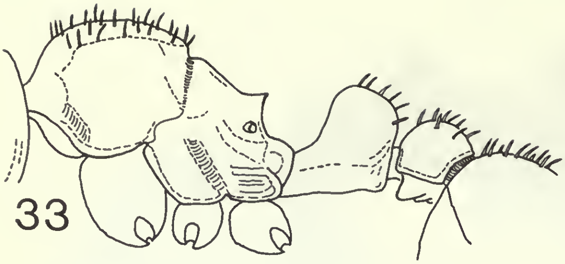

26


27

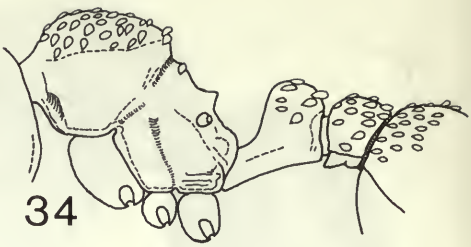

28


29 30 31 32

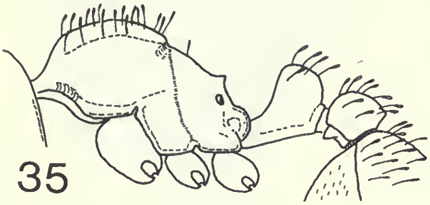
Figs 26–32 *Dicroaspis* and *Calyptomyrmex* workers. 26, Lateral view of *D. laevidens*. 27. Head of *D. laevidens*. 28. Head of *C. barak*, pilosity omitted. 29–32. First gastral tergite to show pilosity of (29) *C. nummuliticus*, (30) *C. arnoldi*, (31) *C. tensus*, (32) *C. foreli*; offsets of 30–32 show approximate shapes of hairs.



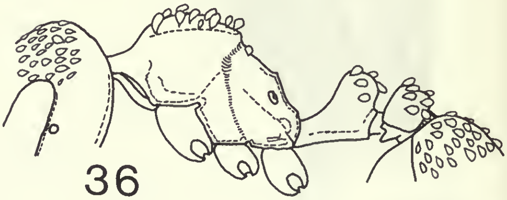
33



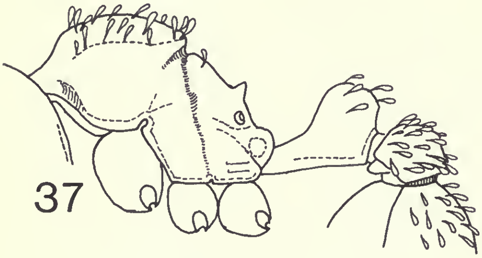
34



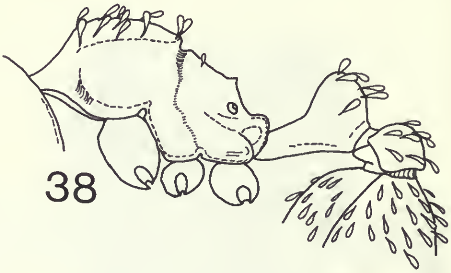
35



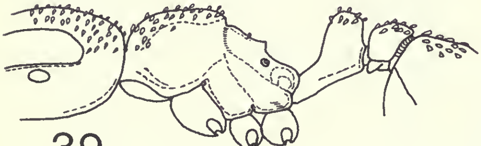
36



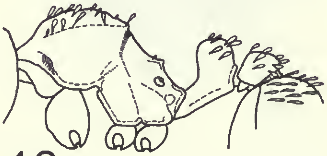
37



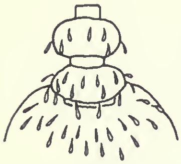
38



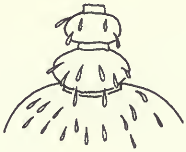
39



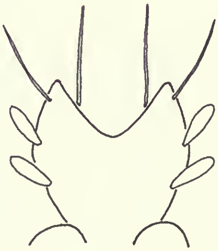
40



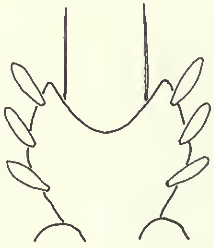
41



42



43



44

Figs 33–44 *Calyptomyrmex* workers. 33–40. Alitrunk and pedicel segments of (33) *barak*, (34) *nummuliticus*, (35) *rennefer*, (36) *piripilis*, (37) *duhun*, (38) *shasu*, (39) *arnoldi*, (40) *tensus*. 41, 42. Dorsal view of pedicel segments in (41) *clavatus*, (42) *clavisetus*. 43, 44. Pilosity of clypeal fork (diagrammatic) in (43) *duhun*, (44) *piripilis*.

Index

Synonyms are in *italics*.

affinis 52
arnoldi 66

barak 62
bondroiti 55
brevis 63
brunneus 70

Calyptomyrmex 59
cataractae 65
clavatus 70
clavisetus 71
clypeatus 52
Cryptocephalus 47
cryptocera 58

Dicroaspis 56
diversipilosus 55
duhun 72

emeryi 67
excisus 56

foreli 67

Geognomicus 56
glaber 49

hartwigi 67

inermis 52

kaurus 64
kiboshana 52

laevidens 59
litoralis 65

magrettii 55
Meranoplus 46

nanior 52
nanus 53
nedjem 68
nitidiventris 55
nummuliticus 68

peringueyi 56
piripilis 65
punctatus 65
pusillus 67

rennefer 72
reticulatus 68

shasu 73
similis 52
simoni 55
soriculus 52
spininodis 50
springvalensis 55
stellatus 69
sthenus 50
suturalis 55

tensus 74

Weberidris 59
wheeleri 58

British Museum (Natural History) Publications

Catalogue of the Diptera of the Afrotropical Region

Editor: R. W. Crosskey. *Assistant editors:* B. H. Cogan,
P. Freeman, A. C. Pont, K. G. V. Smith and the late H. Oldroyd.
British Museum (Natural History). 1980, 1437 pp.   £55·00

The Diptera or two-winged flies are probably the most important insects that affect man. Although most flies are harmless, some have become transmitters of dangerous diseases to man and his domestic animals, and others are important pests of agricultural crops. Some flies are beneficial because they destroy large numbers of plant-feeding insects through their parasitic or predacious habits.

Nowhere is their socio-economic and medical impact more sharply felt than in tropical Africa, where fly-borne diseases are not only a direct health hazard but can prevent or hinder development of the land. The control of such diseases as sleeping sickness and onchocerciasis depends in great measure upon controlling the flies that carry them. This in turn requires a thorough appreciation of all that is known about the insect vectors, including their basic taxonomy, so that they can be correctly identified and their geographical ranges accurately established.

This catalogue synthesizes the scattered basic taxonomic work on the Diptera of tropical Africa and its islands by listing the known 16,500 species with their synonyms and known geographical ranges within a comprehensive classification. A short introduction is given to each family and a bibliography of 4,700 titles provides references to the primary literature. Such a task has never before been attempted for the region and its completion should greatly stimulate taxonomic research. The *Catalogue* represents ten years' careful work by a team of forty specialists, under the editorship of six dipterists on the staff of the Natural History Museum, themselves contributors with considerable expertise in the African fauna.

The *Catalogue* should serve for a long time as an indispensable tool to the taxonomist and an essential source-work to anyone concerned with African flies in the fields of medical, agricultural and veterinary science.

Titles to be published in Volume 42

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. By Michael C. Day.

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. By Barry Bolton.

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). By J. Mark Ritchie.

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). By Angoon Lewvanich.

Printed by The Whitefriars Press Ltd, London and Tonbridge

BRIT
GENERA
- 5 MAY
LIBRARY
NATURAL HIST

Bulletin of the
British Museum (Natural History)

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae)

J. Mark Ritchie

Entomology series
Vol 42 No 3

30 April 1981

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each Volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Ent.)

© Trustees of the British Museum (Natural History), 1981

ISSN 0524-6431

Entomology series
Vol 42 No 3 pp 83–183

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 30 April 1981

GENERAL
- 5 MAY 19
LIBRARY

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae)

J. Mark Ritchie K

Centre for Overseas Pest Research, College House, Wrights Lane, London W8 5SJ

Contents

Synopsis . . . 83
Introduction . . . 83
History of the genus *Oedaleus* . . . 84
Materials, methods and terminology . . . 85
Depositories . . . 86
Oedaleus Fieber . . . 86
  Taxonomic affinities and diagnostic characters . . . 87
  Keys to the species of *Oedaleus* . . . 90
    African species . . . 92
    Non-African species . . . 93
  Descriptions of the species . . . 94
Biogeography of the genus *Oedaleus* . . . 153
  Relationships within the genus . . . 153
  Geographical origin of the genus . . . 153
  The Pleistocene in Africa . . . 154
  The southern African *Oedaleus* fauna . . . 154
  The *Oedaleus* fauna of the Somali peninsula . . . 159
  The *Oedaleus* fauna of the subsaharan latitudinal belt . . . 159
  The non-African *Oedaleus* fauna . . . 163
  Problems of analysis of distribution patterns . . . 168
  East African acridid diversity . . . 169
  The *Brachystegia* woodland and 'trans-equatorial' speciation . . . 169
  The woodland barrier and the 'arid corridor': evidence from other groups . . . 171
  Conclusions . . . 174
Acknowledgements . . . 174
References . . . 175
Index . . . 182

Synopsis

The economically important grasshopper genus *Oedaleus* is revised. Twenty species and three subspecies are described, keyed and illustrated. *O. nadiae*, *O. plenus browni* and the male of *O. miniatus* are described as new to science. Four species and five subspecies are synonymized and two species are reduced to subspecies, one being transferred from the genus *Gastrimargus*. All available primary types have been examined and four neotypes have been designated. Five lectotypes for senior synonyms and seven for junior synonyms have been designated. The biology and economic importance of the species are reviewed and their distributions are mapped. The biogeography of the genus is discussed in the light of past and present geological, vegetational and climatic factors. The fluctuations of the equatorial *Brachystegia* woodland zone in Africa during the Pleistocene are advanced as an explanation of the observed trans-equatorial speciation in *Oedaleus* and some other dry savannah organisms.

Introduction

In recent years members of the genus *Oedaleus* have increasingly been designated as crop pests in Africa, India and South East Asia. The most serious damage has been caused by *Oedaleus*

Bull. Br. Mus. nat. Hist. (Ent.) **42** (3): 83–183 Issued 30 April 1981

senegalensis, a widespread and economically important species, reviewed by Batten (1969). The growing list of described species, and their possible economic importance, have highlighted the lack of any comparative taxonomic and biogeographical study and the need for accurate identification and a more certain knowledge of relationships within the genus. Descamps (1972), speaking at the International Study Conference on the Current and Future Problems of Acridology, included *Oedaleus* among a short-list of genera urgently in need of revision.

This study is intended to facilitate accurate identification of all *Oedaleus* species by agriculturists, ecologists and entomologists involved in locust control and crop protection. To guarantee stable nomenclature, all available primary types have been examined, and neotypes have been designated to replace lost types. In cases where a holotype was not originally designated, lectotypes have been selected from the syntype series. Keys to, and descriptions of all the species and subspecies are included, with figures to illustrate the more important morphological characters. Accurate distribution maps have been compiled, based largely upon data from the labels of the many thousands of specimens examined. Supplementary data have been obtained from correspondents and from reliable published sources. The biogeography of the genus is discussed in the light of known past and present geological, vegetational and climatic features, and the available information on the life histories, biology and economic importance is assembled.

History of the genus *Oedaleus*

The genus *Oedaleus* was erected as a subgenus of *Oedipoda* by Fieber (1853) to accommodate *Acrydium nigrofasciatum* De Geer, 1773. Stal (1873) made *Oedaleus* a subgenus of *Pachytylus* Fieber, 1853 and added to it three species now included in *Gastrimargus,* as well as *Gryllus Locusta flavus* Linnaeus, 1758 and *Gryllus abruptus* Thunberg, 1815. He also synonymized *Gryllus arcuatus* Thunberg, 1824 with *Oedaleus nigrofasciatus* (De Geer, 1773), a fact overlooked by both Kirby (1910) and Johnston (1956).

Saussure (1884) gave *Oedaleus* full generic status and divided it into two subgenera, *Oedaleus* s. str., and the newly-erected *Gastrimargus.* He described *Oedaleus infernalis* and transferred *Pachytylus senegalensis* Krauss, 1877, but placed *Oedaleus flavus* (Linnaeus, 1758) in the genus *Humbella.* Unfortunately, he later (Saussure, 1888) described the same insect as *Oedaleus nigrofasciatus* var. *citrinus* and, despite the use of the older name by Karsch (1887) and Kirby (1902*a*), Saussure's name remained in common use as *Oedaleus citrinus* Saussure (Distant, 1892) until the synonymy was revealed by Dirsh (1961*a*). Linnaeus (1758) assumed that his *Gryllus Locusta flavus* was identical with the *'Locusta capensis alis inferioribus luteis'* described by Petiver (1702) but in the absence of surviving material Petiver's figure cannot definitely be proved to represent this species. *Gryllus Locusta flavus* was wrongly identified with *Acrydium nigrofasciatum* De Geer, 1773, by De Geer himself and by several subsequent authors, although Kirby (1910) pointed out that the *Gryllus flavus* of Fabricius, 1775, a junior synonym of *Oedaleus nigrofasciatus,* should not be considered identical with the *G. L. flavus* of Linnaeus, known to Kirby as *Humbe flava.* He was also aware that the *G. L. flavus* of Stoll (1813) was not the same species as that of Linnaeus, and synonymized it (incorrectly) with *Oedaleus arcuatus* (Thunberg, 1824), which was itself a synonym of *Oedaleus nigrofasciatus* unbeknown to him.

This situation was further complicated by the fact that *Oedaleus nigrofasciatus,* a purely South African species, was always confused with the Mediterranean *Oedaleus decorus* (Germar, 1826), the older name being used indiscriminately until Uvarov (1923) finally demonstrated the separate identity of the two species. Since then some confusion of *O. decorus* and *O. nigrofasciatus* has continued (Hollande, 1926; Jovančić, 1953; Barbut, 1954; Rungs, 1962). *Oedaleus australis* Saussure, 1888, originally described as *O. nigrofasciatus* var. *australis* and given specific status by Kirby (1910), has also been the subject of some confusion. It was frequently identified as *O. senegalensis* (Krauss, 1877) (Froggatt, 1903; 1907; 1910; Sjöstedt, 1920; 1921; Zacher, 1925; 1949), although Uvarov (1930*a*) gave reasons for believing the Australian species to be distinct from the African one.

Kirby (1910) synonymized *Ctypohippus arenivolans* Butler, 1881 and *Pachytylus mlokoziewiztcki*

Bolívar, 1887 with *O. senegalensis*. Distant (1892) transferred *Epacromia plena* Walker, 1870 to *Oedalus* [sic], and Uvarov (1925) synonymized *O. nigrofasciatus* var. *caffer* Saussure, 1888 with this species and transferred *Chortoicetes interruptus* Kirby, 1902 to *Oedaleus*. Throughout the last century numerous new species and subspecies have been described, notably by Uvarov (six species), but there has not been any revisionary treatment of the genus and nomenclatural changes have been limited to those outlined above.

At the commencement of the present study 24 species and four subspecific taxa were recognized.

Materials, methods and terminology

Measurements used in this study generally follow Dirsh (1953) except that total length is here defined as the distance from the frons to the apices of the folded tegmina, as used by Jago (1963), not to the end of the abdomen as used by Dirsh and several other authors; head width is here measured across the genae (Dirsh, 1953) or across the eyes (Jago, 1963), whichever is the larger. The forewing is referred to as the tegmen, not the elytron. All measurements are given in millimetres and were made with Mauser dial calipers graduated with 0.05 mm divisions.

The male genitalia figured in this study were removed and treated in the manner described by Dirsh (1956*b*). Female spermathecae were examined by removal of the posterior abdominal segments and maceration in 10% potassium hydroxide solution. The abdomen was then slit open along the lateral intersegmental membrane to display the spermatheca. After examination genitalia preparations were placed in 70% alcohol with a little glycerine, contained in a polythene vial with a silicone rubber stopper pinned to the appropriate insect specimen.

Abbreviations of terms used in the descriptions and figures of the male genitalia are as follows: A – ancorae of epiphallus; Ac – arch of cingulum; Ap – anterior projections of epiphallus; Apv – apical valves of penis; Apd – apodemes of cingulum; B – bridge of epiphallus; Bp – basal valves of penis; Cv – cingular valves; Dp – dorsal process of cingulum; Ejd – ejaculatory duct; E – ejaculatory sac; Gpr – gonopore process; L – lophi of epiphallus; Lp – lateral plate of epiphallus; Pp – posterior projections of epiphallus; Rm – rami of cingulum; Sps – spermatophore sac. These and most other morphological terms relating to acridids are described and illustrated by Dirsh (1965). Since the genitalia of all species are very similar only those of *O. senegalensis* (Figs 60–64) have been labelled.

The nomenclature of the female spermatheca used in this study is that of Dirsh (1957). The term 'apical diverticulum' is thus understood to denote the bulbous blind-ending sac at the distal extremity of the spermathecal duct. In *Oedaleus* and other Acrididae this may be simple or it may possess a secondary diverticulum, which is usually much smaller. The apical diverticulum is always strongly recurved at its proximal end, and always continues in the direction of the coiling of the duct. The secondary or preapical diverticulum, on the other hand, when not reduced to a mere vestige, projects from the main duct at right angles on the outside of the coil. Since the secondary diverticulum is always smaller than the main seminal reservoir and is often absent, it is reasonable to refer to it as 'preapical' and to the larger diverticulum as 'apical'. However, Slifer (1939), a pioneer of the comparative study of the spermatheca, and other authors have used exactly the opposite designations, thus introducing some confusion. Recently Amedegnato (1976) has confirmed the nomenclature of Dirsh, used here, on the grounds that in the primitive condition there is only one diverticulum which should therefore be called apical.

The terminology of the venation used here is that of Ragge (1955). Except where otherwise stated, material examined is from the collections of the British Museum (Natural History), London.

To save space the label data for material examined of the commoner species have been abbreviated to country and locality only, excepting data for type-material which are given in full. For *O. senegalensis* and *O. decorus decorus* only countries are listed. A full list of all the material of *Oedaleus* species examined during the course of the study has been deposited in the British Museum (Natural History) and the Centre for Overseas Pest Research.

Distances and altitudes are given in SI units whatever the units of the original source.

Depositories

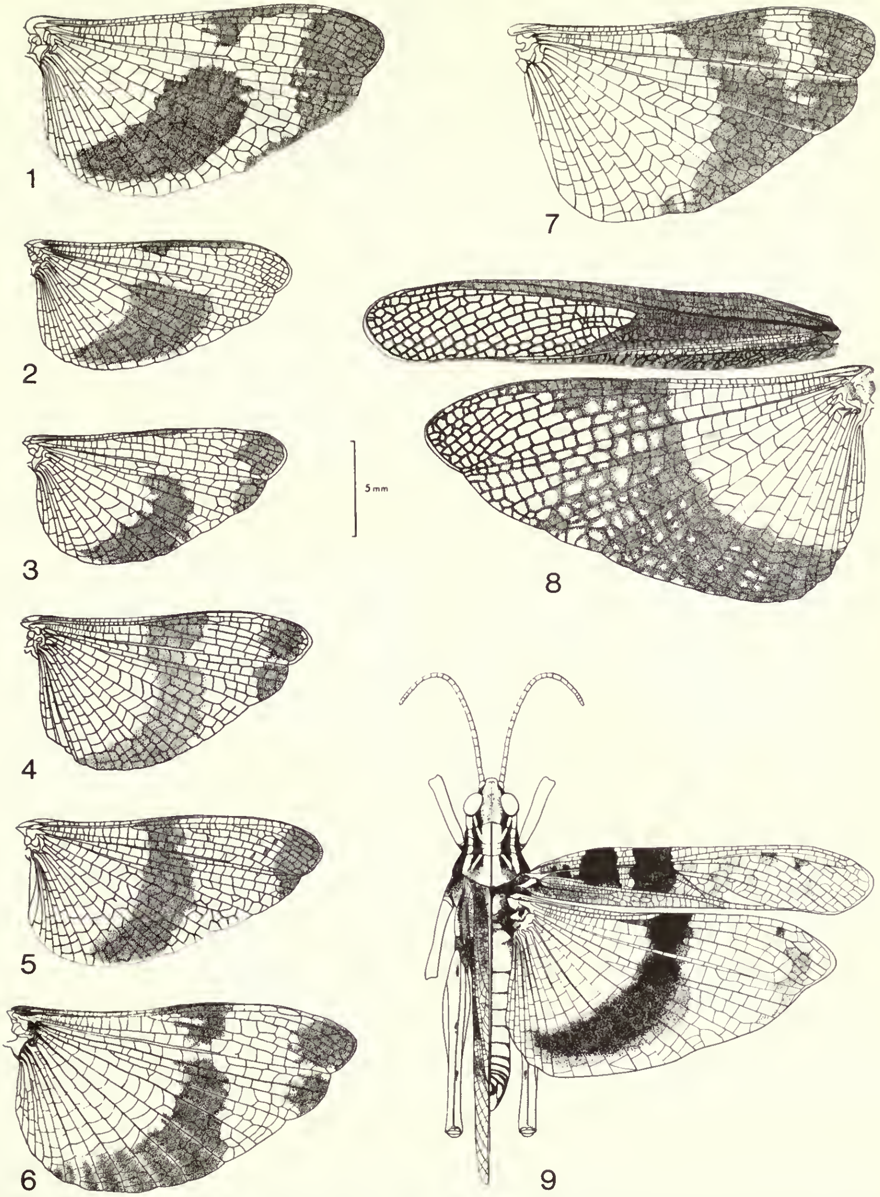
MA, Addis Ababa	Ministry of Agriculture, Addis Ababa.
MNHU, Berlin	Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin.
ANIC, Canberra	Australian National Insect Collection, Canberra.
MHN, Geneva	Muséum d'Histoire Naturelle, Geneva.
MCSN, Genoa	Museo Civico di Storia Naturale, Genoa.
BPBM, Honolulu	Bernice P. Bishop Museum, Honolulu.
ZI, Leningrad	Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad.
MLZA, Lisbon	Museu e Laboratório Zoológico e Antropológico, Universidade de Lisboa, Lisbon.
BMNH	British Museum (Natural History), London.
COPR, London	Centre for Overseas Pest Research, London.
UM, Oxford	Hope Entomological Collections, University Museum, Oxford.
MNHN, Paris	Muséum National d'Histoire Naturelle, Paris.
ANS, Philadelphia	Academy of Natural Sciences, Philadelphia.
DATS, Pretoria	Department of Agricultural Technical Services, Pretoria.
CAS, San Francisco	California Academy of Sciences, San Francisco.
NR, Stockholm	Naturhistoriska Rijksmuseum, Stockholm.
ZIUU, Uppsala	Zoologiska Institutionen, Uppsala Universitet, Uppsala.
NM, Vienna	Naturhistorisches Museum, Vienna.
USNM, Washington	United States National Museum, Washington.

OEDALEUS Fieber

Oedaleus Fieber, 1853: 126 [as subgenus of *Oedipoda* Serville]. Type-species: *Acrydium nigrofasciatum* Degeer, 1773, by monotypy.
Oedaleus Fieber; Stål, 1873: 123 [as subgenus of *Pachytylus* Fieber].
Oedaleus Fieber; Saussure, 1884: 50.

Medium size (total length: 20–44 mm in male, 25–49 mm in female). Integument rugose and pitted. Fastigium of vertex angular with truncate apex, flat or slightly concave, with obtuse lateral carinulae variable in emphasis, with or without median longitudinal carinula; fastigial foveolae obsolete. Antennae (except in *O. miniatus*) filiform, as long as, or longer than length of head and pronotum together. Frons in profile oblique, convex, straight, or concave; frontal ridge sulcate with marginal carinulae diverging ventrally, reaching or not reaching clypeus. Eyes elongate-oval to oval, long axis vertical. Pronotum from high tectiform to saddle-shaped, constricted anterior to and at junction of prozona and metazona, wider and with distinct 'shoulders' in metazona; median carina linear, often intersected by posterior transverse sulcus; raised lateral carinae absent in most species, occasionally present in prozona underlying anterior arms of X-marking; metazona equal to or little longer than prozona, rarely (in *O. interruptus*) much longer, posterior margin rounded or angular; mesosternal interspace wider than long, widening posteriorly, usually wider than metasternal interspace. Tegmina and wings fully developed, or only slightly abbreviated; intercalary vein of medial area of tegmen well developed and finely serrate, at least in males, continuing to distal apex of medial area; membrane of tegmen semi-transparent with variable reticulation in basal half. Hind femur slender or broad, exterior ventral knee lobe acutely rounded; hind tibia as long as femur, apical spurs not specialized; arolium of medium size or small. Male supra-anal plate shield-shaped, rounded triangular; cercus conical, apically acutely rounded, of variable length; subgenital plate (except in *O. miniatus*) short, subconical with rounded apex; epiphallus bridge-shaped with well-developed ancorae and large, bilobate lophi; ectophallic membrane sclerotized and forming sheath below apical penis valves; cingulum with horseshoe-shaped arch bearing moderately long apodemes; cingular valves acute, less sclerotized than apical penis valves; basal penis valves with anterior lateral expansions, sometimes recurved, flexure narrow; apical penis valves short, acute, with serrated ventral subapical process. Female ovipositor short, valves robust, vertically excurved; spermatheca with sac-like apical diverticulum with or without a short preapical diverticulum.

General coloration variable, greenish or brownish with contrasting light and dark markings. Genae of head with oblique light and dark markings. Pronotum with variable dorsal light markings in the form of an X, lacking central intersection and divided into four arms by median carina and posterior transverse sulcus. Anterior arms of X often continued anteriorly onto head, crossing or not crossing eyes as a pale longitudinal stripe. Lateral lobes of pronotum with distinct white oblique marking centrally, sometimes reaching hind margin. Tegmina and hind femora with corresponding transverse light and dark bands, variable, sometimes obscure. Hind wing weakly or strongly tinted with yellow, pink, or red, usually but not always bounded by a dark fascia; remainder

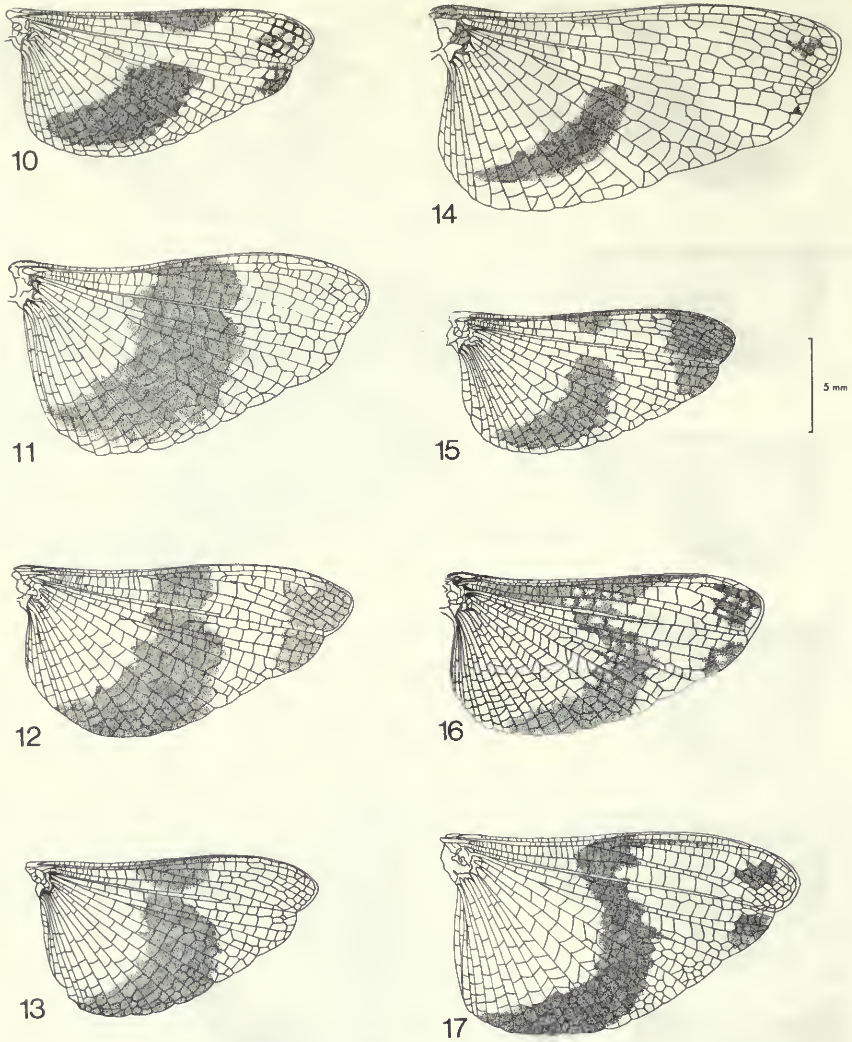


Figs 1–9 *Oedaleus* species (males), wings 1, *O. australis;* 2, *O. abruptus;* 3, *O. obtusangulus;* 4, *O. rosescens*; 5, *O. infernalis*; 6, *O. plenus plenus*; 7, *O. formosanus*; 8, *O. senegalensis* (melanic); 9, *O. senegalensis* (normal).

of wing transparent, colourless, sometimes apically darkened. Interior surface of hind femur straw-coloured, red, or mauve; tibiae red, straw-coloured, or grey.

Taxonomic affinities and diagnostic characters

Oedaleus falls naturally within the subfamily Oedipodinae, recently reinstated by Dirsh (1975). It comprises a homogeneous group of species found widely in the Old World tropics and subtropics. It may be distinguished from related genera by a combination of the following characters: the presence of a wing band in most species, the form and markings of the pronotum, the hind femur having the



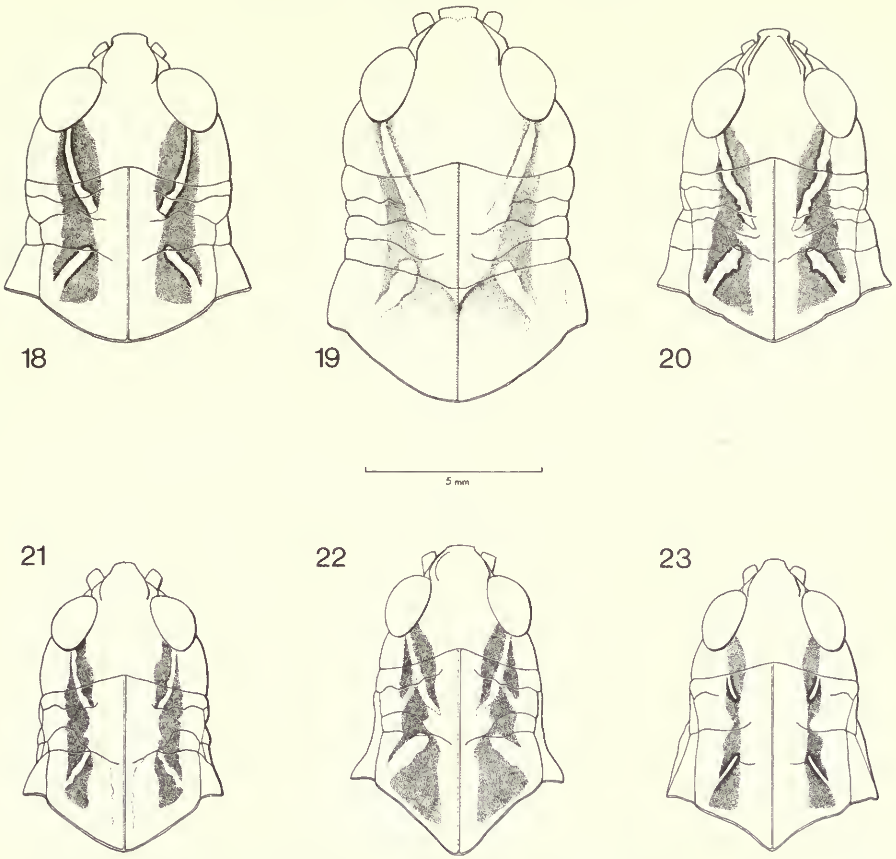
Figs 10–17 *Oedaleus* species (males), wings. 10, *O. nigeriensis*; 11, *O. decorus decorus*; 12, *O. instillatus*; 13, *O. interruptus*; 14, *O. johnstoni*; 15, *O. carvalhoi*; 16, *O. miniatus*; 17, *O. flavus*.

upper marginal area not excised and lower marginal area not expanded, the tegmen lacking specialized stridulatory veinlets and by the short apical penis valves. It may be distinguished from the closely related genus *Gastrimargus* Saussure by the following key.

1 Pronotal X-marking with anterior and posterior arms continuous; posterior arms usually curved and with slightly convergent apices. Hind margin of pronotum rectangular to acutangular, never rounded . . . . ***GASTRIMARGUS***

– Pronotal X-marking always with anterior and posterior arms separate; posterior arms straight, not converging. Hind margin of pronotum rounded to rectangular, never (except in *O. interruptus, O. miniatus,* and some *O. plenus*) acutangular . . . . ***OEDALEUS***

As indicated by the rather poor characters given above, there are no reliable objective criteria for separating the genera *Oedaleus* and *Gastrimargus* in their entirety one from the other. However, all the species presently considered as members of either of these genera are more closely allied to their congeners than to any member of the other genus. Saussure (1884) separated out *Gastrimargus* as a



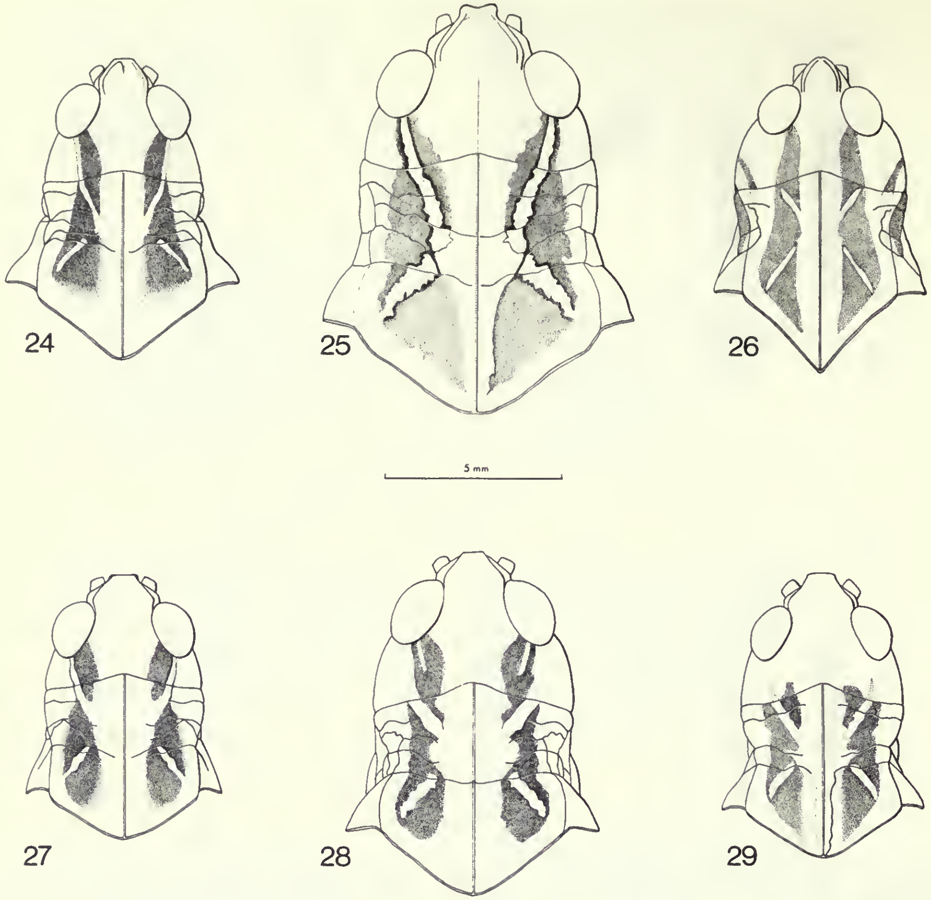
Figs 18–23 *Oedaleus* species (females), heads and pronota, dorsal view. 18, *O. senegalensis*; 19, *O. johnstoni*; 20, *O. nigeriensis*; 21, *O. nigrofasciatus*; 22, *O. plenus* (brown form); 23, *O. carvalhoi* (green form).

subgenus of *Oedaleus* largely on the basis of an overall impression of stoutness in the former. *Gastrimargus* later rose to generic status without any reasoned defence of its elevation (Kirby, 1910).

Saussure himself and later authors have sometimes experienced difficulty in referring marginal species to one genus or the other.

It is probable (but not yet certain) that all or most species of *Oedaleus* possess a pronotal repugnatorial gland and that, by contrast, *Gastrimargus* species do not. This may in the future give a more certain separation between the two genera. At present the division is workable and convenient since it enables the separation of 40 or so species into two almost equal groups of species with distinct ecological preferences. It appears that *Oedaleus* species are basically characteristic of sub-desert steppes and dry grasslands while *Gastrimargus* species are found in more humid wooded savannahs and tall grass.

Despite the uniformity of morphology within the genus, useful characters for species identification can be obtained by close examination. These include the shape and patterning of the dorsal surface of the pronotum (Figs 18–38), the banding or lack of banding on the hind wing (Figs 1–17), and the coloration of the ventral surface of the hind femora. The male genitalia offer some useful supporting characters which may, however, be difficult to interpret. In the females some additional information can be gained by studying the ventral surface of the ovipositor valves (Figs 39–59). However, the spermatheca is of little value for identification, being variable within one species and rather uniform within the genus as a whole.



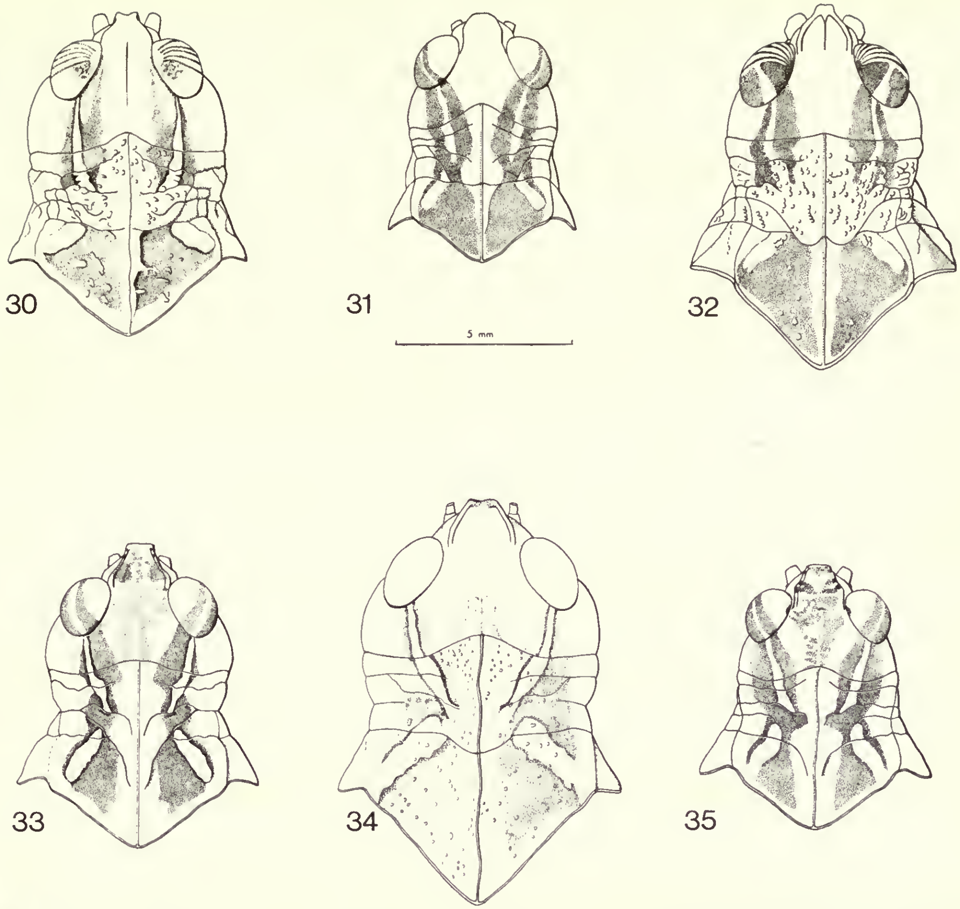
Figs 24–29 *Oedaleus* species (females), heads and pronota, dorsal view. 24, *O. virgula* (brown form); 25, *O. inornatus*; 26, *O. interruptus*; 27, *O. australis*; 28, *O. decorus decorus* (green form); 29, *O. decorus asiaticus* (brown form).

Keys to the species of *Oedaleus*

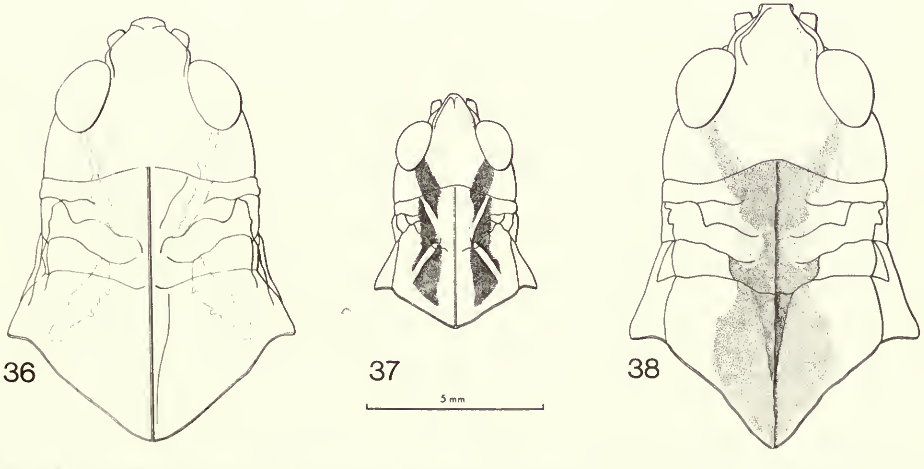
These are the first keys designed to facilitate the identification of all the known species of the genus *Oedaleus*. Keys to *Oedaleus* species occurring in eastern Asia were published by Chang (1939) and by Bei-Bienko & Mishchenko (1951*b*) but these are of little value since insufficient attention was paid to the examination of type-material and assessment of the range of infra-subspecific variation. Succeeding students of the subject have uncritically adopted the erroneous judgements of earlier authors with the result that the keys presently in use serve merely to distinguish imaginary taxa by the use of thoroughly unreliable characters. Thus the subspecies *O. infernalis pendulus* Steinmann (1965) was distinguished from other supposed subspecies largely on the basis of the proportions of the medial antennal segments. I am indebted to L. L. Mishchenko (pers. comm.), who has seen the type, for the information that it is in fact a junior synonym of *Dociostaurus maroccanus* (Thunberg).

For brevity and ease of use, two keys are here provided, one covering Africa and its islands, Arabia and Madagascar, and the other dealing with the rest of the old world. In this way a specimen from Asia can be identified without needing to compare it with more than a dozen species which are known to be restricted to the Ethiopian Region. Some widespread species occur in both keys, and variable species are keyed out twice in the same key.

As in some other recent generic revisions in the Acrididae, for example that of *Aiolopus* Fieber by Hollis (1968), the male phallic complex has been found to display considerable uniformity. For this



Figs 30–35 *Oedaleus* species (females), heads and pronota, dorsal view. 30, *O. nadiae*; 31, *O. rosescens*; 32, *O. miniatus*; 33, *O. instillatus*; 34, *O. flavus*; 35, *O. obtusangulus*.



Figs 36–38 *Oedaleus* species (females), heads and pronota, dorsal view. 36, *O. infernalis*; 37, *O. abruptus*; 38, *O. formosanus*.

reason, although they are described and figures elsewhere in this study, genital characters have not been used to construct a separate key for males. Instead one key is given for both sexes with the main characters derived from the shape and markings of the pronotum, the form of the hind wing fascia, and the colour of the basal area of the hind wing and the interior surface of the hind femur. In addition, characters from the genitalia of either sex are used as subordinate evidence of identification where appropriate.

In these keys total length and head width have been used as subsidiary characters even if the known size-ranges of two taxa partially overlap.

African species

1 Hind wing pink or red basally . . . 2

– Hind wing bright yellow or pale yellow basally . . . 3

2 (1) Hind wing with basal area scarlet in male, salmon pink in female, bounded by distinct brown fascia (Fig. 16); antennae flattened, ensiform; male subgenital plate with medial dorso-posterior process (Figs 132, 133) (Somalia, E. Kenya) . . ***O. miniatus*** Uvarov (p. 142)

– Hind wing with basal area clear rose pink in both sexes, lacking fascia; antennae filiform; male subgenital plate normal (N. Somalia) . . . ***O. nadiae*** sp. n. (p. 145)

3 (1) Hind wing fascia continuous to tip of wing; tegmen unicolorous brown, without pattern (Fig. 8) (Cape Verde Is.) . . . melanic form of ***O. senegalensis*** (Krauss) (p. 94)

– Hind wing fascia forming a distinct band, never continuous to wing tip; tegmen speckled or banded, never unicolorous brown . . . 4

4 (3) Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9, 11) 5

– Hind wing fascia broadly interrupted, indistinct, or absent . . . 9

5 (4) Hind wing basally bright yellow; dorsal surface of pronotum with small light brown warts (Fig. 34); hind femur internally mauve to deep violet (except E. African males) (S. and E. Africa) ***O. flavus*** (Linnaeus) (p. 149)

– Hind wing basally pale yellow to colourless; dorsal surface of pronotum smooth; hind femur never mauve or violet internally . . . 6

6 (5) Hind femora ventrally straw-coloured; hind margin of pronotum rounded or parabolic 7

– Hind femora ventrally red or reddish brown; hind margin of pronotum rectangular to obtusangular . . . 8

7 (6) Hind margin of pronotum parabolic (Fig. 18); bridge of epiphallus with acutely curved interior surface (Figs 62, 63) (W. Africa to E. Africa N. of 8°S.) . . . ***O. senegalensis*** (Krauss) (p. 94)

– Hind margin of pronotum oval (Fig. 21); bridge of epiphallus with obtusely curved interior surface (Fig. 68) (Southern Africa S. of 17°S.) . . ***O. nigrofasciatus*** (Degeer) (p. 99)

8 (6) Small species, total length: 22·0–27·5 mm male, 30·0–37·5 mm female; general coloration mottled brown or grey; head, pronotum, and hind femora occasionally pale green suffused with brown, tegmina never tinged with green; white transverse bars on tegmen reduced, not reaching second cubital vein (E. Africa) . . . ***O. instillatus*** Burr (p. 136)

– Large species, total length: 29·0–45·5 mm male, 42–53 mm female; general coloration variable, green, straw, or brown, always broken up by bands of darker pigment; dorsal surface of folded tegmina suffused with green in green specimens; white transverse bars on tegmina always reaching to second cubital vein (N. Africa) . ***O. decorus*** (Germar) (p. 122)

9 (4) Hind wing fascia absent or only faintly visible . . . 10

– Hind wing fascia distinctly visible but widely interrupted around first anal vein 12

10 (9) Large robust species, total length: 26·8–37·1 mm male, 33·5–48·5 mm female, head width: 4·3–5·4 mm male, 5·8–7·8 mm female (E. Africa) . ***O. inornatus*** Schulthess (p. 147)

– Small species, total length: 22·0–29·0 mm male, 29·0–40·0 mm female, head width: 3·0–4·0 mm male, 4·0–5·5 mm female . . . 11

11 (10) Pronotal X-marking variable but never absent, posterior arms of X thick (Fig. 22); ventral surface of hind femora red, tegmina exceeding hind knees by one-quarter of femur length or less; female posterior ventral basivalvular sclerite smooth, pale, unsclerotized, lightly pitted (Fig. 45) (Eastern S. Africa) . . extreme form of ***O. plenus browni*** subsp. n. (p. 121)

– Pronotal X-marking thin, often indistinct, sometimes absent; ventral surface of hind femur

brown, never red; tegmina exceeding hind knees by one third of femur length or more; female posterior ventral basivalvular sclerite dark, sclerotized, and with rugose warts (Fig. 42) (Madagascar) . . . . . ***O. virgula*** (Snellen van Vollenhoven) (p. 107)
12 (9) Large species, head width 4·5–5·2 mm male, 5·8–7·6 mm female; general coloration pale, uniform, mottled, usually sandy, occasionally suffused with pale green; pronotal X-marking indistinct, pronotal median carina weak, seldom raised, hind margin of pronotum evenly rounded, never angular (Mauritania to Ethiopia) . . ***O. johnstoni*** Uvarov (p. 109)
– Smaller species, head width 3·5–4·6 mm male, 4·5–6·5 mm female; general coloration darker, with contrasting lighter markings on pronotum and tegmina; pronotal X-marking distinct, pronotal median carina strongly marked, slightly arcuate, hind margin of pronotum angular 13
13 (12) Tibiae and ventral surface of hind femora straw-coloured, never red . . 14
– Tibiae and ventral surface of hind femora red or orange-red 15
14 (13) Pronotal hind margin forming an obtuse angle with concave sides (Fig. 23), pronotal X-marking very fine; hind wing fascia strongly marked (Fig. 15) (Southern Africa) . . . ***O. carvalhoi*** Bolivar (p. 116)
– Pronotal hind margin forming a flat or convex-sided right angle (Fig. 35), pronotal X-marking thicker; hind wing fascia weakly marked (Fig. 3) (Aïr Mts, Niger, and Arabia) . . ***O. obtusangulus*** Uvarov (p. 138)
15 (13) Hind margin of pronotum sharply acute, pronotal X-marking very thin; eyes seen from above small and close set, vertex narrow (Fig. 26); dark pattern of tegmina separated into rounded cells; hind wing fascia widely expanded and rounded anteriorly (Fig. 13) (Transvaal) ***O. interruptus*** (Kirby) (p. 134)
– Hind margin of pronotum bluntly rectangular or obtusangular, pronotal X-marking variable but thicker; eyes normal, more widely set; vertex broader (Figs 20, 22); dark pattern of tegmina forming bands separated by narrow lighter areas; hind wing fascia narrowing or narrowly expanded anteriorly 16
16 (15) Hind margin of pronotum forming right angle or obtuse angle with concave sides (Fig. 22); hind wing fascia, when complete, not widening in anterior half (Fig. 6), often incomplete, failing to reach second anal vein, occasionally absent (Southern Africa and Tanzania) . . ***O. plenus*** (Walker) (p. 118)
– Hind margin of pronotum forming a flat or convex-sided angle (Fig. 20); hind wing fascia widening anteriorly, reaching to second anal vein (Fig. 10) (Senegal to Ethiopia and South to Tanzania) . . . . ***O. nigeriensis*** Uvarov (p. 112)

Non-African species

1 Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9, 11) 2
– Hind wing fascia broadly interrupted 6
2 (1) Hind wing basally pale pink (Fig. 4) (Pakistan, NW. India) . . ***O. rosescens*** Uvarov (p. 141)
– Hind wing basally pale yellow, or pale greenish yellow, in *O. decorus* tinged with pale blue at base of main veins 3
3 (2) Hind wing fascia continuous posteriorly with dark markings at wing tip (Fig. 7); pronotal X-marking indistinct, forming boundary to medial diamond-shaped dark area and merging laterally with lighter markings on sides of pronotum (Fig. 38); tegmen uniformly dark brown, light transverse bands absent or reduced to anterior edge of wing (Taiwan) . ***O. formosanus*** (Shiraki) (p. 132)
– Hind wing fascia not continuous posteriorly with dark markings at wing tip; pronotal X-marking variable, sometimes obscured, but not merging laterally with lighter markings on sides of pronotum; tegmen with two light transverse bands always present . . 4
4 (3) Hind margin of pronotum rounded, subarcuate (Fig. 18); ventral surface of hind femur never suffused with red (Arabia, Iran, Pakistan, W. India) . ***O. senegalensis*** (Krauss) (p. 94)
– Hind margin of pronotum bluntly obtusangular; ventral surface of hind femora suffused with red 5
5 (4) Pronotal X-marking sharply outlined, anterior and posterior arms of equal width (Fig. 28); hind wing fascia always dark and well defined (S. Europe, Middle East, U.S.S.R., China, Mongolia) . . . . ***O. decorus*** (Germar) (p. 122)

– Pronotal X-marking often indistinct, sometimes absent, posterior arms thicker than anterior arms (Fig. 36); hind wing fascia variable, light brown, edges ill-defined (Fig. 5) (SE. U.S.S.R., E. China, Japan) . . . . **O. infernalis** Saussure (p. 128)

6 (1) Anterior termination of hind wing fascia flattened, reaching or just surpassing second anal vein; fascia, particularly in male, often pale, posterior two thirds parallel to posterior edge of wing; wing narrow (Fig. 2); fastigium of vertex narrow, with lateral carinulae distinct, sharply converging (Fig. 37) (Pakistan, Nepal, India, Bangladesh, Indo-China, China) . . **O. abruptus** (Thunberg) (p. 104)

– Anterior termination of hind wing fascia rounded, surpassing second anal vein, almost reaching first anal vein; fascia distinct, not parallel to edge of wing, wing tip in male heavily clouded; wing normal (Fig. 1); fastigium of vertex broader, carinulae less marked, less convergent (Fig. 27) (SE. New Guinea, Australia, Tasmania) . . **O. australis** Saussure (p. 101)

Descriptions of the species

Oedaleus senegalensis (Krauss, 1877)
(Figs 8, 9, 18, 40, 60–65, 160)

Pachytylus senegalensis Krauss, 1877: 56. Syntypes ♂♀, SENEGAL: St Louis & Dagana (*F. Steindachner*) (lost). NEOTYPE ♂, SENEGAL (BMNH), here designated [examined].

Ctypohippus arenivolans Butler, 1881: 85. Holotype ♀, CAPE VERDE IS. (BMNH) [examined]. [Synonymized by Kirby, 1910: 225.]

Pachytylus mlokoziewiztcki Bolívar, 1884: 105. LECTOTYPE ♂, U.S.S.R.: Tiflis (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1921: 487.]

Oedaleus mlokosiewitchi (sic) (Bolívar) Bolívar, 1887: 98; Jacobson & Bianchi, 1902: 256.

Oedaleus (*Oedaleus*) *mlokozievetsi* (sic) (Bolívar); Saussure, 1888: 40.

Oedaleus (*Oedaleus*) *mlokozievetzi* (sic) (Bolívar); Saussure, 1888: 42.

Oedaleus (*Oedaleus*) *senegalensis* var. *c*. Saussure, 1888: 42; Uvarov, 1921: 487.

Oedaleus mlokosiewiczi (sic) (Bolívar); Jacobson & Bianchi, 1902: 188.

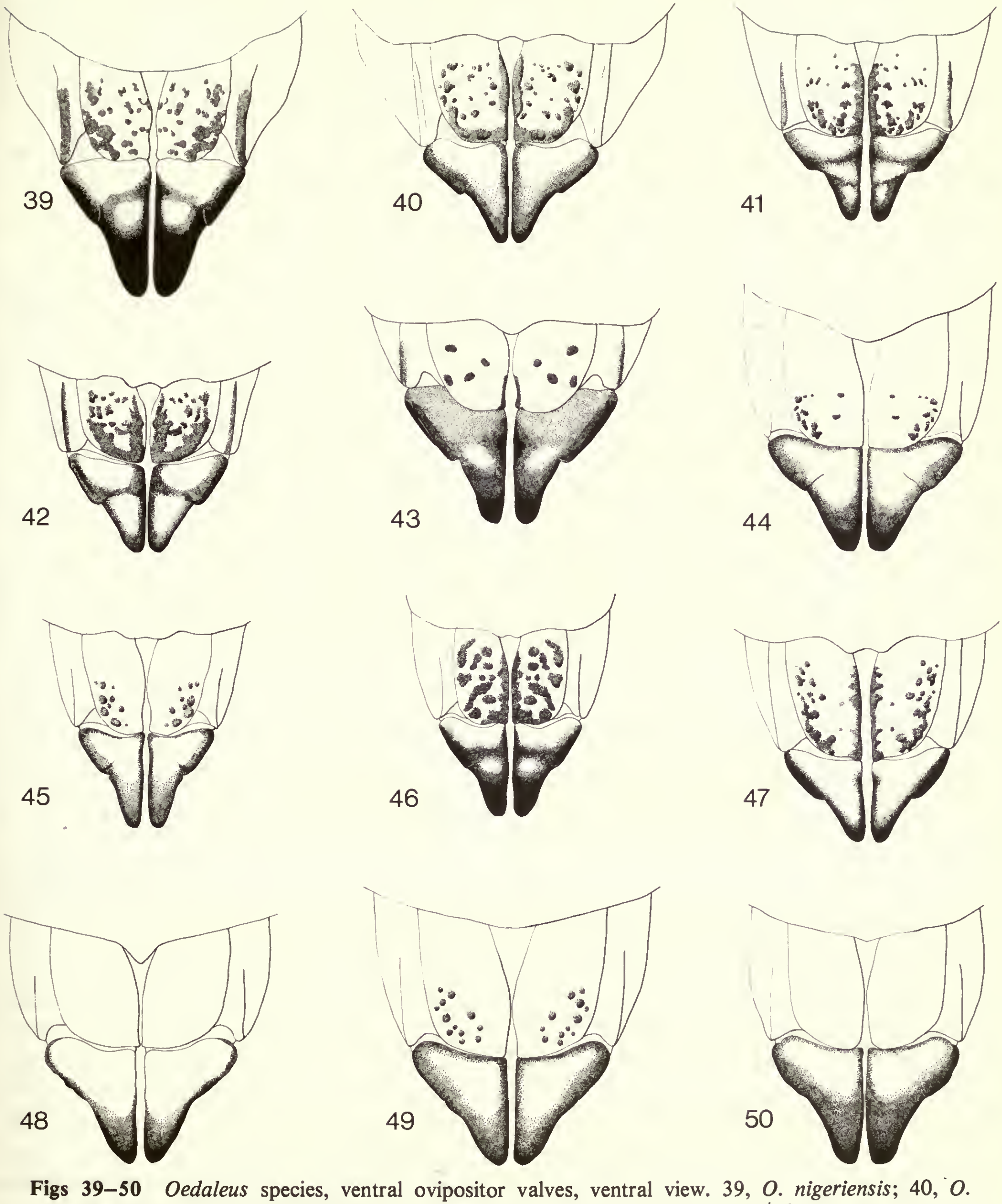
Oedaleus senegalensis (Krauss); Bolívar, 1889: 104.

Oedaleus senegalensis var. *dimidiatus* Bolívar, 1889: 105. Holotype ♀, CAPE VERDE IS. (MLZA, Lisbon) [examined]. **Syn. n.**

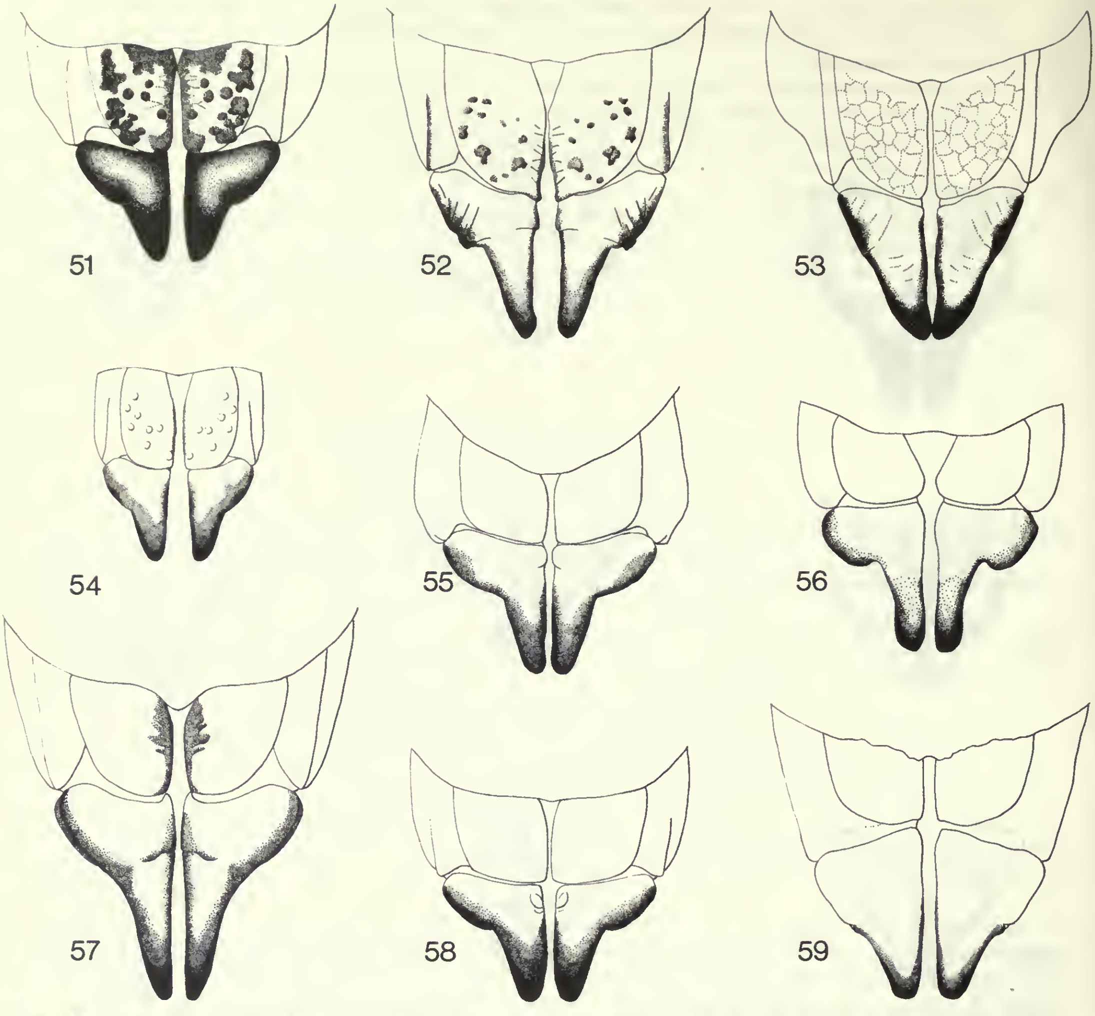
REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae up to twice as long as head and pronotum together, flagellum with 24–26 segments. Fastigium little longer than wide, concave, narrowing to little less than half of maximum width anteriorly, margins raised; frons in profile, slightly convex; frontal ridge barely constricted ventral to median ocellus. Eyes little less than one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, not or barely intersected by posterior sulcus; hind margin subarcuate. Tegmen surpassing folded hind knees by one-third to one-half length of hind femur. Hind tibia with 13 inner and 12–13 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci one and three quarter times as long as basal width. Genitalia (Figs 60–64): cingular apodemes moderate length and thickness; rami fully developed, with exposed portion of cingular and apical penis valves short, subapical ventral process rounded; epiphallus rectangular with narrow bridge; inner lobes of lophi more than twice as wide as outer; anterior projections large, rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal two-fifths, with strong transverse pale band reaching first anal vein one-third along from base; indistinct pale transverse band sometimes visible one-sixth along from base; apical two-fifths of tegmen clear with occasional infumate cells bordered by darkened veins. Hind wing fascia (Fig. 9) complete, sometimes narrowly interrupted between second cubitus and first anal vein, not reaching hind margin of wing; basal area pale yellow, apex very slightly speckled with infumate cells. Hind femora with three indistinct oblique transverse dark bands on outer upper marginal and medial areas extending onto inner surface; ventral surface pale straw-coloured; hind knee dark brown; hind tibia with dark basal ring, subbasal pale straw area then straw shaded with brown and distally pinkish.

♀. Ventral ovipositor valves (Fig. 40) short, well sclerotized. Spermatheca (Fig. 65) with apical diverticulum elongate with short, blunt subapical diverticulum.



Figs 39–50 *Oedaleus* species, ventral ovipositor valves, ventral view. 39, *O. nigeriensis*; 40, *O. senegalensis;* 41, *O. nigrofasciatus;* 42, *O. virgula;* 43, *O. johnstoni;* 44, *O. carvalhoi;* 45, *O. plenus;* 46, *O. interruptus*; 47, *O. australis*; 48, *O. abruptus*; 49, *O. flavus flavus*; 50, *O. flavus somaliensis*.



Figs 51–59 *Oedaleus* species, ventral ovipositor valves, ventral view. 51, *O. decorus*; 52, *O. infernalis*; 53, *O. formosanus*; 54, *O. rosescens*; 55, *O. obtusangulus*; 56, *O. instillatus*; 57, *O. inornatus*; 58, *O. nadiae*; 59, *O. miniatus*.

MEASUREMENTS

Sample from Niger: Danga, at light, 7.viii.74 (*J. M. Ritchie*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27·35	3·87	3·64	20·79	12·57	2·73	4·61	5·71
Range	23·5–30·4	3·4–4·5	3·1–3·4	17·3–23·4	11·1–14·4	2·3–3·1	4·3–5·0	5·0–6·2
S.D.	2·127	0·236	0·278	1·783	0·932	0·175	0·197	0·266
n	24	29	29	24	28	28	28	24

Females

Mean	35·38	5·04	4·55	26·97	15·61	3·3	4·74	5·96
Range	30·3–39·0	4·4–°·5	3·6–5·3	23·2–30·0	13·3–17·7	2·9–3·8	4·1–5·1	5·3–6·6
S.D.	1·726	0·222	0·33	1·493	0·807	0·201	0·216	0·317
n	42	45	45	42	45	45	45	42

Sample from Niger: Danga, at light, 12.ix.74 (*J. M. Ritchie*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	32·64	4·60	4·56	24·56	15·53	3·39	4·59	5·44
Range	31·2–34·8	4·2–5·0	4·1–5·1	22·7–26·7	13·2–17·1	3·0–3·7	4·2–4·8	4·8–5·9
S.D.	1·15	0·231	0·295	1·042	0·879	0·156	0·139	0·499
n	18	19	19	18	20	20	20	18

Females

Mean	42.39	6·12	5·77	32·16	19·6	4·28	4·58	5·99
Range	40·4–46·9	5·7–6·5	5·1–6·5	30·7–35·2	17·7–21·3	3·9–4·6	4·2–5·0	4·9–6·0
S.D.	1·551	0·204	0·382	1·095	0·938	0·199	0·189	0·295
n	20	20	20	20	20	20	20	20

AFFINITIES. *O. senegalensis* is most closely allied to *O. nigrofasciatus* from southern Africa. They may be distinguished with difficulty on grounds of size, pronotal shape (Figs 18, 21), and the shorter anal cerci of male *senegalensis* (Fig. 64). Both species belong to a close-knit group of species characterized by an epiphallus having lophi with large, transverse, inner lobes much larger than the outer lobes.

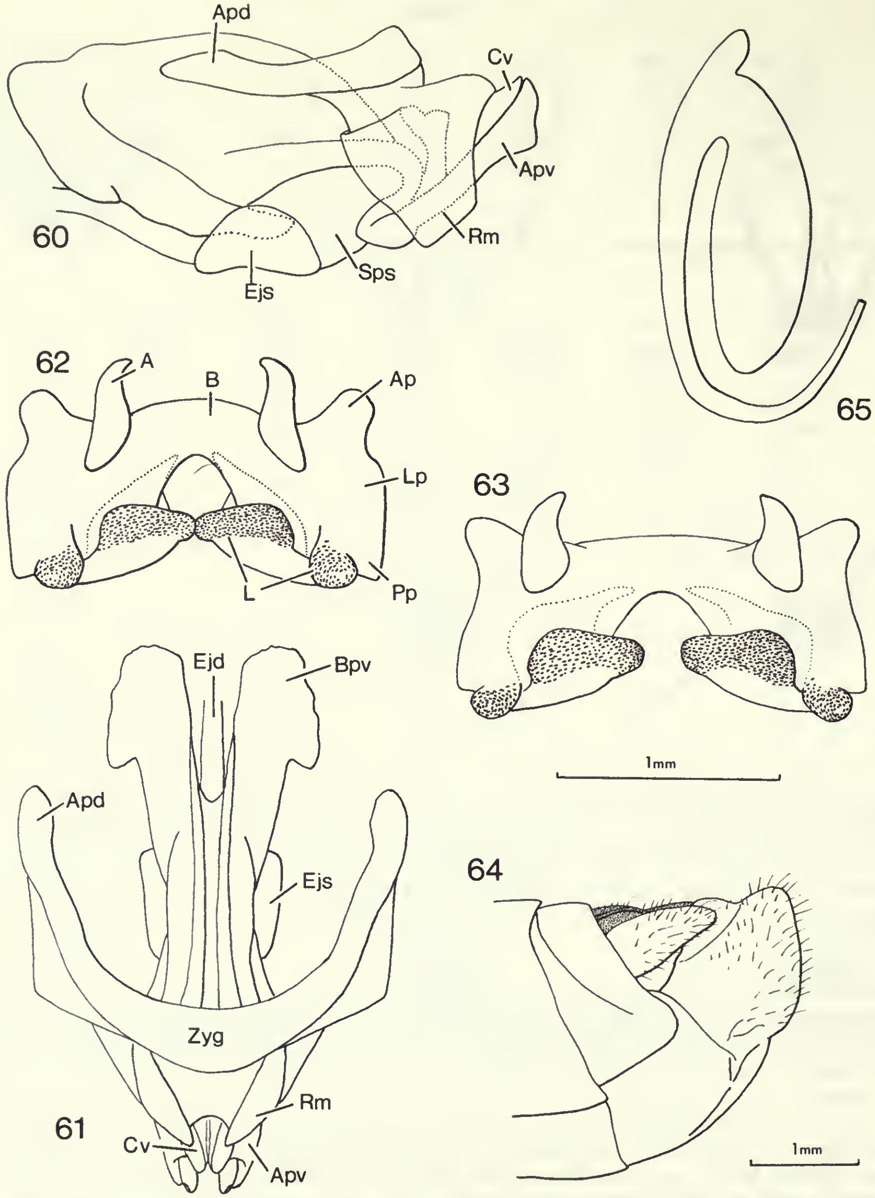
MATERIAL EXAMINED

Pachytylus senegalensis Krauss, neotype ♂, **Senegal:** Dakar airport, at light, 6.x.1974 (*Ritchie*) (BMNH). *Ctypohippus arenivolans* Butler, holotype ♀, **Cape Verde Is.:** St Vincent I., from sandy patches, 24.x.1878 (*Butler*) (BMNH). *Pachytylus mlokoziewiztcki* Bolivar, lectotype ♂, **U.S.S.R.:** Tibilisi ('Tiflis'), no further data (MHN, Geneva). *Oedaleus senegalensis* var. *dimidiatus* Bolivar, holotype ♀, **Cape Verde Is.:** (*Ferreira Borges*) (MLZA, Lisbon).

In addition to the primary type-material listed above, more than 3500 specimens were examined from the following countries: **Canary Is., Cape Verde Is.** (including material of var. *dimidiatus*), **Gambia, Senegal, Mauritania, Algeria, Mali, Niger, Nigeria, Sudan, Ethiopia, Somali Republic, Kenya, Tanzania, Socotra, Yemen, Saudi Arabia, Kuwait, Qatar, Israel, Jordan, Syria, Iran, Afghanistan, Pakistan, India.**

DISTRIBUTION (Fig. 160, and Biogeography section, p. 162). From the Canary Is. in the west, across north and subsaharan Africa, into the western U.S.S.R. in the north-east and western India in the south-east.

BIOLOGY. The available data on the life history, distribution, ecology, and economic importance of this species were reviewed by Batten (1969). More recently Lecoq (1978) has investigated the life cycle in relation to migration in Upper Volta, and Launois (1979) has advanced a theoretical model of the annual cycle consisting of three generations with latitudinal movements governed by the Intertropical Convergence Zone. Launois-Luong (1976) has made estimates of fecundity by a detailed study of the ovaries and Cheke, Fishpool & Ritchie (1980) have studied the distribution and predation of egg pods, giving descriptions of the pod, the eggs, and oviposition behaviour. The influence of rainfall in terminating egg diapause has been investigated by Venkatesh et al. (1971). The



Figs 60–65 *O. senegalensis*, genitalia. 60, endophallus and cingulum, lateral view; 61, same, dorsal view; 62, 63, variation in epiphallus shape; 64; apex of male abdomen, lateral view; 65, spermatheca.

occurrence of large numbers of *O. senegalensis* out at sea off the West African coast has been documented by Ritchie (1978*a*). The thoracic repugnatorial gland has been described by Vosseler (1902*c*), and the causes of colour change by Abushama & El Khider (1973). Several birds are known to prey on this species including the carmine bee-eater, *Merops nubicus* (Nickerson, 1958), the Abyssinian roller, *Coracias abyssinicus* (Roy, 1970), and the cattle egret, *Ardeola ibis* (pers. obs.). Since 1973 there have been several unpublished reports describing crop damage and aspects of the biology of *O. senegalensis* (Popov, 1974; McAleer, 1977; Page, 1977).

Discussion. The variety *dimidiatus* Bolivar from the Cape Verde Is. is here synonymized on the grounds that it is sympatric with the normal form of *O. senegalensis* and almost certainly constitutes a melanic variant rather than a good subspecies. A fuller treatment of this subject with measurements of the two forms have been given elsewhere (Ritchie, 1978*a*). The measurements given above for this species form part of a study of the morphometric changes in this species during the 1974 rainy season in north-western Niger (Ritchie, unpubl.). They illustrate the considerable size differences which may be encountered in this species within a small geographical area over a short period of time.

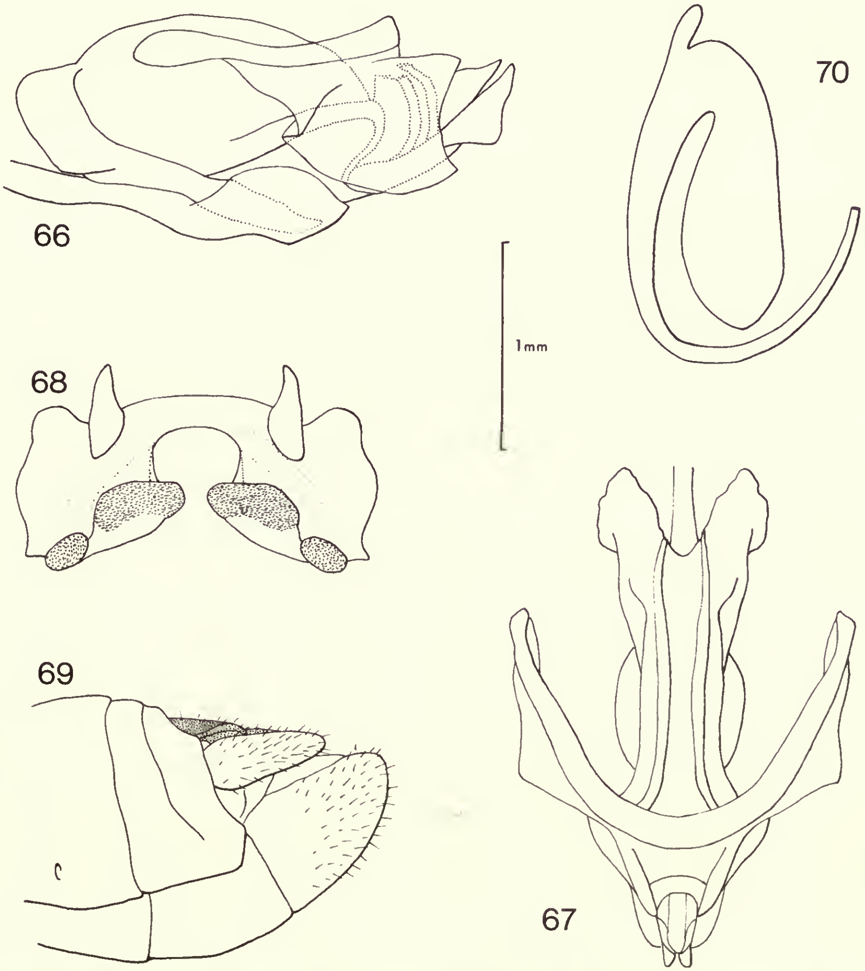
The type-material of *Pachytylus mlokoziewiztcki* Bolivar comprises one male, here designated lectotype, and one female, designated paralectotype.

Oedaleus nigrofasciatus (Degeer, 1773)
(Figs 21, 41, 66–70, 152)

Acrydium nigrofasciatum Degeer, 1773: 493. Holotype ♀, South Africa (NR, Stockholm) [examined].

Gryllus arcuatus Thunberg, 1824: 409. LECTOTYPE ♂, no data (ZIUU, Uppsala) here designated [examined] [Synonymised by Stål, 1873: 126.]

Pachytylus nigrofasciatus (Degeer) Schaum, 1853: 776. [Partly confused with *Oedaleus decorus* (Germar).]



Figs 66–70 *O. nigrofasciatus*, genitalia. 66, endophallus and cingulum, lateral view; 67, same, dorsal view; 68, epiphallus; 69, apex of male abdomen, lateral view; 70, spermatheca.

Pachytylus (*Oedaleus*) *nigro-fasciatus* (Degeer); Stål, 1873: 126. [Partly confused with *Oedaleus decorus* (Germar).]
Oedaleus (*Oedaleus*) *nigro-fasciatus* (Degeer) Saussure, 1884: 116.
Oedaleus (*Oedaleus*) *nigro-fasciatus* var. *gracilis* Saussure, 1884: 116. LECTOTYPE ♀, SOUTH AFRICA: Cape of Good Hope (MHN, Geneva), here designated [examined]. [Partly confused with *Oedaleus decorus* (Germar).] [Synonymized by Uvarov, 1923: 69.]
Oedalus [sic] *nigrofasciatus* (Degeer); Distant, 1892: 260.
Oedaleus nigrofasciatus var. *gracilis* Saussure; Saussure, 1893: 581.
Oedaleus nigrofasciatus (Degeer); Brancsik, 1900: 182.
Oedaleus nigrofasciatus (Degeer); Kirby, 1910: 224. [Partly confused with *Oedaleus decorus* (Germar).]
Oedaleus gracilis Saussure; Uvarov, 1922: 102.

REDESCRIPTION. ♂. Integument finely rugulose and punctate. Antennae one and a half times as long as head and pronotum together; flagellum with 23 segments. Fastigium longer than wide, concave with lateral margins distinct and convergent posteriorly, narrowing to two-fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus, becoming obsolete ventrally. Eyes about one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, often finely intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by one-third to one-half of hind femur length. Hind tibiae with 12 inner and 11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times claw length; arolium three-fifths of claw length. Cerci twice as long as basal width. Genitalia (Figs 66–69): cingular apodemes thin, moderately long and curved; rami elongate dorsally; exposed portion of cingular and apical penis valves short; subapical ventral process angular; epiphallus rectangular with narrow bridge, inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded, posterior projections small and acute.

General coloration variable, brown, with lighter brown, ochraceous, or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal half with three irregular pale transverse bands at intervals of one-sixth, one-third, and one-half, along from base, basal band often obsolete; apical half clear with small variable brown patches. Hind wing fascia as in *O. senegalensis*, continuous, not touching hind margin; wing tip with irregular pattern of brown cells; basal area pale yellow. Hind femur with three dark brown variable oblique transverse bands on external medial, upper marginal, and interior upper marginal areas, obsolescent on interior medial area; ventral surface mid brown, hind knees dark brown to black; hind tibiae with dark basal ring, subbasal pale area, otherwise fawn.

♀. Ventral ovipositor valves (Fig. 41) short, moderately sclerotized, slightly incurved on external lateral surface. Spermatheca (Fig. 70) with finger-like subapical diverticulum.

MEASUREMENTS
Sample from South Africa: Cape Province, various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26·52	3·47	3·89	20·17	12·44	2·85	4·38	5·20
Range	23·3– 30·2	3·1– 3·9	3·1– 4·8	17·5– 23·5	10·8– 13·8	2·4– 3·2	4·05– 4·6	4·6– 5·9
S.D.	1·557	0·190	0·383	1·295	0·766	0·182	0·164	0·299
n	27	26	27	27	27	27	27	27

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	32·99	4·58	4·97	25·15	15·67	3·48	4·50	5·07
Range	29·8– 35·6	4·2– 4·9	4·3– 5·6	22·7– 27·0	13·8– 17·2	3·0– 3·8	4·2– 4·8	4·7– 5·7
S.D.	1·755	0·208	0·375	1·375	0·964	0·202	0·189	0·255
n	13	13	13	13	13	13	13	13

AFFINITIES. *O. nigrofasciatus* is most closely allied to *O. senegalensis* under which species heading the principal similarities are described (p. 97).

MATERIAL EXAMINED

Acrydium nigrofasciatum Degeer, holotype ♀, **South Africa:** Cape of Good Hope, no further data (NR, Stockholm). *Gryllus arcuatus* Thunberg, lectotype ♂, no data (ZIUU, Uppsala). *Oedaleus nigrofasciatus* var. *gracilis* Saussure, lectotype ♀, **South Africa:** Cape of Good Hope, no further data (MHN, Geneva).

In addition to the primary type-material listed above, 211 specimens were examined from the following localities. **South Africa:** Transvaal, Reitspruit; T., Johannesburg; T., Pretoria; T., Zeerust, Morico; 32·2 km NE. of Pretoria; T., 96·6 km NE. of Ermelo; T., Lydenburg distr.; T., Waterburg distr.; T., Platrivier; T., Potchefstroom; T., Makokoane; Orange Free State: Bloemfontein to Port Elizabeth; O.F.S., Bloemfontein; O.F.S., Boshof; O.F.S., Witzieshoek, 1830 m; North Bank Halt, Norvals Pont; O.F.S., Ficksburg; Natal, Zululand, Nqutu; N., Natal National Park; Cape Province, Middleburg; C.P., Knysna, Plettenburg Bay; C.P., Albert distr., Simonstown; C.P., Ceres; C.P., Worcester; C.P., Aliwal North; C.P., Rondenbosch; C.P., Contour Path; C.P., Huguenot; C.P., Traddow Pass; C.P., Mafeking; C.P., Swellendam: C.P., Cape Peninsula, Signal Hill; C.P., Newlands; C.P., Mossel Bay; C.P., Kirstenbosch; C.P., Du Toit's Kloof, nr Paarl; C.P., Waterval-Onder; C.P., Namaqualand; C.P., 20 km SW. of Mitchell's Pass; C.P., Highlands, Grabon; C.P., Stellenbosch; C.P., Hopetown; C.P., Citrusdale to Clan William road. **Namibia:** Okahandja; Okahandja to Waterberg; 17°59′S, 16°02′E, 1110 m; Rietfontein, 19°50′S, 17°52′E; Otjikoko Süd Farm, 53·1 km ENE. of Omaruru; Otjitambi Farm, 43·5 km ESE. of Kamanjab; Hoffnung Farm, 16·1 km NE. of Windhoek. **Botswana:** Lobatsi; Ghanzi; Mongalatsiba; Kwebe Hills; Ngamiland; Gaberones; Kuke Pan; Kaotwe; Metsimaklaba. **Zimbabwe:** Odzi distr.; Selukwe, 1420 m; Matopo Hills; Mutambara; West Nicholson, Masase.

DISTRIBUTION (Fig. 152, and Biogeography section, p. 156). Widely distributed and common throughout southern Africa south of the *Brachystegia* woodland.

BIOLOGY. *O. nigrofasciatus* has been studied in the Karroo where Reyneke (1941) noted that the species has similar habitat preferences to the brown locust *Locustana pardalina* (Walker). It was found in open sandy or pebbly patches with short grass and scattered shrubs at an average density of five insects per square metre. Nymphs were seen from the end of September until November. In the Cape peninsula Key (1930) found adults from November to June and observed oviposition from January to June. Egg pods were 21–24 mm long with 15–19 eggs, and were usually curved and medially constricted. In Johannesburg Chesler (1938) found somewhat larger pods, about 29 × 5 mm with 20–25 eggs in rows of four. Chesler described the five nymphal instars which occupied an average of 80 days for their completion. She postulated a two-generation cycle with eggs hatching in September to produce adults November–December whose eggs hatched in January to give a second generation of adults in April. These adults then lay eggs which remain in the soil until the next rains in September. Nolte (1939) compared the biology of *O. nigrofasciatus* with six other common species of grasshopper including *O. carvalhoi*. He reported that adult females of *O. nigrofasciatus* have 15 ovarioles per ovary. Both *Oedaleus* species were found to have the standard acridid complement of 11 pairs of autosomes and an XO sex determination system. There is one record of damage to tobacco seedlings in Rhodesia (Bünzli & Buttiker, 1956).

DISCUSSION. The type-series of *Gryllus arcuatus* Thunberg comprises one male, here designated lectotype, and one female, designated paralectotype. *O. nigrofasciatus* var. *gracilis* Saussure was described from South Africa and south Russia. In the MHN, Geneva, there are two males and two females labelled as *gracilis* from South Africa as well as several specimens from Russia which are actually *O. decorus*. A single female from South Africa bears the labels 'Cap. B. Esp.' and '*nigrofasciatus* Th. var. *gracilis* Sss. Afr.', apparently in Saussure's own handwriting. This specimen is here designated lectotype. No paralectotypes have been designated because of uncertainty as to whether Saussure himself named the remaining specimens when he was describing var. *gracilis*.

Oedaleus australis Saussure, 1888
(Figs 1, 27, 47, 71–74, 164)

Oedaleus (*Oedaleus*) *senegalensis* var. *d*. Saussure, 1884: 117; Uvarov, 1930*d*: 599.

Oedaleus (*Oedaleus*) *nigro-fasciatus* var. *australis* Saussure, 1888: 41. LECTOTYPE ♀, AUSTRALIA (MHN, Geneva), here designated [examined].

[*Oedaleus senegalensis* var., Froggatt, 1903: 1105. Misidentification; Uvarov, 1930*d*: 599.]

[*Oedaleus senegalensis* Krauss; Froggatt, 1907: 539; 1910: 7. Misidentifications: Uvarov, 1930*b*: 599.]

Oedaleus australis Saussure; Kirby, 1910: 225.
[*Oedaleus senegalensis* Krauss; Sjöstedt, 1920: 11. Misidentification; Uvarov, 1930*d*: 599.]
[*Oedaleus senegalensis* Krauss; Sjöstedt, 1921: 53. Misidentification.]
[*Oedaleus senegalensis* Krauss; Zacher, 1925: 204; 1949: 298. Misidentifications; Batten, 1969: 29.]
Oedaleus australis var. *plana* Sjöstedt, 1931*a*: 2. Holotype ♀, AUSTRALIA: A.C.T., Canberra, 20.ii.29 (*Fuller*) (ANIC, Canberra). **Syn. n.**

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to less than one third of maximum width anteriorly, with well-defined lateral carinae; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus. Eyes about one and a third times as deep as wide. Pronotum low tectiform; median carina arcuate, narrowly intersected by posterior sulcus; hind margin of pronotum rounded obtusangular. Tegmen surpassing folded hind knees by one-quarter to one-half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer; apical tarsal segment three times length of claw; arolium one-third length of claw. Cerci little more than twice as long as basal width. Genitalia (Figs 71–73) with cingular apodemes long, thin, strongly curved; rami fully developed, with exposed portion of cingular and apical penis valves short; subapical ventral process small; epiphallus rectangular with narrow bridge; inner lobes of lophi nearly twice as wide as outer; anterior projections large, rounded acutangular; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal half with irregular pale transverse band extending from costal margin to second anal vein posteriorly, situated one-third along from base; indistinct secondary band sometimes visible one-sixth along from base; apical half of tegmen clear with variable brown patches. Hind wing fascia (Fig. 1) narrowly interrupted at first anal vein, not reaching hind margin of wing; wing tip infuscate brown, basal area of wing pale yellow. Hind femora with three indistinct dark, variable, oblique transverse bands on outer and inner upper marginal and medial areas; ventral surface of hind femur straw-coloured; hind knees blackish; hind tibiae with dark basal ring, subbasal pale area, otherwise light brown.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 47) short, strongly sclerotized, with strongly curved apices. Spermatheca (Fig. 74) with apical diverticulum acutely rounded distally and finger-like subapical diverticulum.

MEASUREMENTS (all available material)

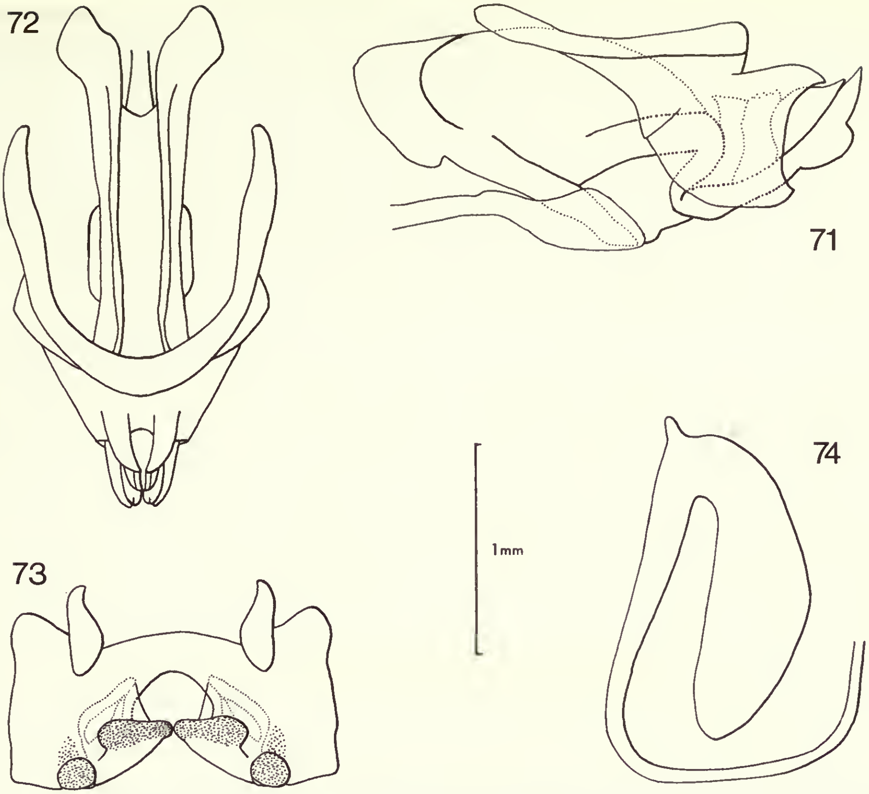
Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	24·13	3·71	3·73	17·59	12·5	3·05	4·11	4·74
Range	20·0–27·8	3·1–4·1	2·8–4·2	14·2–20·9	10·5–14·3	2·6–3·5	3·7–5·0	3·8–5·6
S.D.	2·371	0·299	0·377	2·034	1·085	0·223	0·347	0·539
n	11	12	12	12	12	12	12	12

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31·09	4·93	4·99	23·02	15·3	3·8	4·03	4·63
Range	28·6–34·5	4·2–5·6	3·7–6·1	20·0–26·2	13·6–16·6	3.3–4·2	3·8–4·2	4·2–5·3
S.D.	1·712	0·305	0·479	1·562	0·84	0·222	0·113	0·328
n	18	22	21	21	21	21	21	21

AFFINITIES. *O. australis* is most closely allied to *O. senegalensis* and *O. nigrofasciatus* which it very closely resembles in most respects, and with which it was originally confused. It may be distinguished by its smaller size, the interrupted band of the hind wing (Fig. 1), and the relatively short tegmen and correspondingly low TL/PL ratio.



Figs 71–74 *O. australis,* genitalia. 71, endophallus and cingulum, lateral view; 72, same, dorsal view; 73, epiphallus; 74, spermatheca.

MATERIAL EXAMINED

Oedaleus nigrofasciatus var. *australis* Saussure, lectotype ♀, **Australia** (MHN, Geneva). *Oedaleus australis* var. *plana* Sjöstedt, holotype ♀, **Australia:** A.C.T., Canberra, 20.ii.1929 (*Fuller*) (ANIC, Canberra).

Australia: 1 ♂, Queensland, 20·9 km E, 3 mls N. of Candamine, Nangram lagoon, 14.viii.1954 (*Stirton*) (CAS, San Francisco); 1 ♂, N. Queensland, Ravenshoe–Mt Garnet road, Archer's Creek, 11.i.1962 (*Britton*); 2 ♀, Queensland Dept. Agric., 1954; 2 ♀, Queensland (*Waterhouse*); 1 ♀, N. Queensland, Inkerman, nr Townsville; 1 ♀, Queensland, Peak Downs (MNHU, Berlin); 1 ♀, Queensland, Proserpine, 7.ii.1964 (*Sedlacek*) (BPBM, Hawaii); 1 ♀, Queensland, 24 km S. of Sarina, 7.ii.1964 (*Sedlacek*) (BPBM, Hawaii); 1 ♀, Queensland, Kuranda, 1904 (*Perkins & Koebele*) (BPBM, Hawaii); 1 ♂, Queensland, Brisbane, 16.ii.1915 (*Hacker*) (MNHU, Berlin); 1 ♂, Queensland, 24·2 km from Brisbane, Acacia Ridge, 6.iv.1966 (*Grant*); 1 ♂, N.S.W., Shoalhaven R., 27.xi.1948 (*Britton*); 4 ♂, 2 ♀, 1 nymph, 4·8 km W. of Cooma, 28.i.1962 (*Britton*); 1 ♀, N.S.W., Cadramatta, at light, 10.iii.1959 (*Nikitin*); 1♀, N.S.W., Cadramatta, 11.xii.1957 (*Nikitin*); 1 ♀, same data, 1.iii.1958; 2 ♀, N.S.W., Sydney, 26.ii.1902; 1 ♂, 1 ♀, N.S.W., Woy Woy, 8.iii.1924 (*Nicholson*); 1 ♀, N.S.W., Clarence R., (*Lea*); 1 ♂, N.S.W., S. of Coonamble, flat plain pasture, 22.xi.1969 (*Lambert*); N.S.W., Trangie, at light, 1.xii.1969 (*Lambert*); 2 ♀, 4·83 km NE. of Trangie, *E. populifolia* wood and pasturelend, 28.xi.1969 (*Lambert*); 1 ♀, W. central N.S.W., Hillside, NE. of Trangie, at light, 25.xi.1969 (*Cameron*); 1 ♀, N.S.W., no further data (MHN, Geneva) (paralectotype of *O. nigrofasciatus* var. *australis* Saussure); 2 ♀, A.C.T., Paddy's Creek, 25.xii.1965 (*Richards*); 1 ♀, Paramatta, no further data. **Tasmania:** 1 ♂, no further data (*Lea*). **New Guinea:** 1 ♂, Variatara distr., Port Moresby, 18.iii.1956 (*Brown*).

DISTRIBUTION (Fig. 164, and Biogeography section, p. 165). Common throughout the eastern half of Australia, and Tasmania. The species is newly recorded here from New Guinea. Additional data for the distribution map have kindly been provided by Dr K. H. L. Key, from specimens in the Australian National Insect Collection, Canberra.

BIOLOGY. Little is known of the biology of *O. australis*. There are probably at least two generations with eggs surviving the dry season April–September, since adults and nymphs have mainly been recorded September–March. However, adults do occur in all months in suitable localities (ANIC specimens). Large swarms were recorded damaging pasture at Singleton, N.S.W., in 1906–7 (Froggatt, 1907). There was a heavy incidence of an unspecified dipterous parasite. Eggs were laid in well-defined egg beds. In a later account (Froggatt, 1910) egg pods were said to be laid about 32 mm deep in hard clay soil on open grassy ridges with 30–50 eggs per pod. *O. australis* has been recorded among the stomach contents of the straw-necked ibis, *Threskiornis spinicollis* and the white ibis, *T. molucca* (Carrick, 1959). It seems that this species rarely achieves swarm densities.

DISCUSSION. The type of *O. australis* var. *plana* was generally supposed to be at Stockholm. However, I am indebted to Dr Key for the following information:

'There is indeed in Stockholm a specimen determined as *plana* by Sjöstedt and bearing his "Typus" label. But it came from Colosseum, Qld., whereas the only locality given for *plana* in the brief original description of 1931 (under "*Oedaleus senegalensis*") mentions only one locality, namely "Canberra". Thus the Stockholm "type" is not even a syntype. However, the ANIC does have a single female bearing the capture data essentially as cited by Sjöstedt, namely "Canberra F.C.T. 20 Feb. 1929 M. Fuller". It bears also the following labels: (1) "*Oedaleus australis* var. *recta* [sic] Sjöst. det.", and (2) "*Oedaleus senegalensis* Kr. ♀ Yngve Sjöstedt det." The name "*recta*" is a *nomen nudum* and clearly a lapsus for "*plana*", described as "mit *geradem* Kiel des Pronotums." In the absence of evidence that Sjöstedt had more than one specimen before him, the Canberra female, being the only one to bear the required capture data, must be accepted as the holotype. I have now added the following label: "HOLOTYPE ANIC 8747. *Oedaleus australis* var. *plana* Sjöst., 1931. ♀", on red fluorescent card.'

Saussure (1884; 1888) was clearly never able satisfactorily to separate *O. senegalensis, O. nigrofasciatus,* and *O. nigrofasciatus* var. *australis*. In his 1884 work he mentioned material of *O. senegalensis* from 'Australia' which must be *australis* and in 1888 he described *O. nigrofasciatus* var. *australis* from 'Nov. Holland' but also listed a var. *a* of *O. senegalensis* from 'Australia' and a var. *c* from 'Nov. Holl.', both of which are clearly conspecific with *australis*. Neither of the two female specimens of *australis* in Saussure's collection at Geneva is labelled as such. Instead one is labelled '*O. senegalensis* Kr.' and the other '*Acridium maculatum* Br.'. Both are labelled as from Australia, not 'Nov. Holland'. It is possible that Saussure never labelled any material as var. *australis* since his curatorial practice was very variable and he may in any case have been unsure of the identity of his material. Accordingly the female misidentified as *O. senegalensis* is here designated lectotype of *O. nigrofasciatus* var. *australis* and the other female is designated paralectotype.

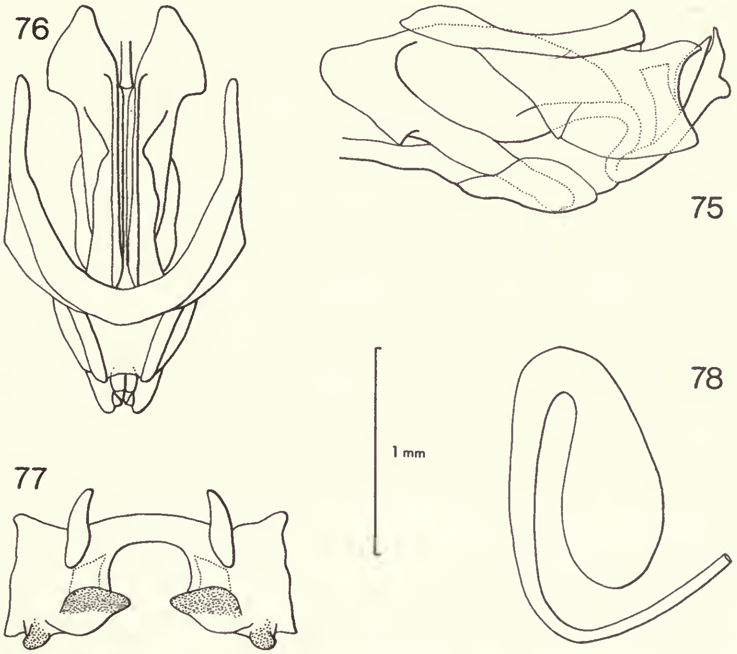
Oedaleus abruptus (Thunberg, 1815)
(Figs 2, 37, 48, 75–78, 157)

Gryllus abruptus Thunberg, 1815: 233. LECTOTYPE ♂, CHINA (ZI, Uppsala) here designated [examined].
Pachytylus (*Oedaleus*) *abruptus* (Thunberg) Stål, 1873: 127.
Oedaleus (*Oedaleus*) *abruptus* (Thunberg) Saussure, 1884: 117.
Oedaleus abruptus (Thunberg); Kirby, 1910: 226.
[*Oedaleus nigrofasciatus* (Degeer); Barber & Jones, 1915: 163; Gabriel, 1968: 101. Misidentifications.]

REDESCRIPTION. ♂. Unusually small species. Integument finely rugulose and pitted. Antennae about one and one-third times as long as head and pronotum together; flagellum with 20 segments. Fastigium of vertex longer than wide, concave, narrowing to two-fifths of maximum width anteriorly, with distinct lateral carinae; frons in profile slightly convex; frontal ridge constricted just below median ocellus, becoming obsolescent ventrally. Eyes about one and two-fifths as long as wide. Pronotum low tectiform; median carina low arcuate, not intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by about one-third of hind femur length with numerous long fine hairs on subcostal and radial veins. Hind tibia with 13 inner and 12 outer spines; inner apical spurs one and four-fifths as long as outer, apical tarsal segment twice claw length; arolium three-fifths length of claw; outer surface of ventral inner apical spur with row of conical sensilla, more marked than in other species. Cerci one and four-fifths times as long as basal width. Genitalia (Figs 75–77) with cingular apodemes long and strongly curved; rami elongated with exposed portion of cingular and apical penis valves short, subapical ventral process small; epiphallus rectangular with narrow bridge; inner lobes of lophi two and a half times as wide as outer lobes; outer lobes outwardly protruding, pointed; anterior projections rounded acutangular; posterior projections acutangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate in basal half with three or four pale transverse bands, variable in emphasis, extending from costal margin to first radial vein or as far as first cubitus, first and second bands dividing basal half of wing equally into three, band three situated distal to junction of *Cu1a* and *Cu1b,* band four situated about two-thirds along from base, frequently obsolete; apical third of tegmen clear with variable brown blotches. Hind wing fascia (Fig. 2) widely interrupted between first radial and second anal veins, reaching or almost reaching hind margin, basal area pale yellow. Hind femora with two indistinct dark transverse bands on external upper marginal and medial areas, sometimes obsolete; internal surface mottled; ventral surface straw-coloured; hind knees dark brown; hind tibiae straw-coloured with dark basal ring and thicker subbasal pale ring.

♀. Ventral ovipositor valves (Fig. 48) strongly sclerotized with strongly curved apices. Spermatheca (Fig. 78) without subapical diverticulum.



Figs 75–78 *O. abruptus,* genitalia. 75, endophallus and cingulum, lateral view; 76, same, dorsal view; 77, epiphallus; 78, spermatheca.

MEASUREMENTS
Sample from Sri Lanka: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	18·97	2·69	3·07	14·27	9·34	2·19	4·26	4·64
Range	17·9–20·2	2·5–2·8	2·8–3·3	13·2–15·3	8·3–10·0	2·0–2·4	4·0–4·7	4·5–4·8
S.D.	1·28	0·090	0·141	0·744	0·526	0·105	0·242	0·103
n	8	8	8	8	8	8	8	8

Females

Mean	24·20	3·65	3·88	18·05	11·48	2·78	4·12	4·64
Range	21·9–26·0	3·2–4·0	3·4–4·4	16·1–20·9	9·7–12·5	2·4–3·0	3·9–4·6	4·4–4·9
S.D.	1·286	0·215	0·284	1·136	0·769	0·157	0·188	0·157
n	14	15	13	15	15	15	15	13

Sample from China: Hainan Province, Wutoshi.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	21·71	2·95	3·36	16·2	10·33	2·25	4·59	4·81
Range	20·4–24·1	2·7–3·1	3·0–3·8	15·0–18·0	9·5–11·7	2·1–2·4	4·3–5·1	4·1–5·2
S.D.	1·042	0·085	0·210	0·796	0·501	0·095	0·189	0·252
n	23	23	21	23	23	23	23	21

Females

Mean	26·88	3·71	4·16	20·0	12·32	2·74	4·51	4·82
Range	25·0–29.7	3·4–4·2	3·5–4·7	18·4–22·2	11·2–14·1	2·4–3·1	4·1–5·0	4·5–5·1
S.D.	1·207	0·180	0·267	0·986	0·713	0·168	0·280	0·167
n	18	18	17	18	16	16	16	17

AFFINITIES. *O. abruptus* is allied to *O. senegalensis* on the basis of its genitalia and general appearance. However, it may easily be distinguished from any other species by its small size and the distinctive hind wing fascia (Fig. 2).

MATERIAL EXAMINED

Gryllus abruptus Thunberg, lectotype ♂, **China:** '*abruptus α*' (ZIUU, Uppsala).

In addition to the primary type-material listed above, 191 specimens were examined from the following localities. **Pakistan:** Rawalpindi; Rawalpindi distr., Kallan, 5100 m; Rawalpindi distr., Sangiani. **India:** Mysore St, 12·9 km SE. of Hassan; Pondicherry St, Karikal; Coimbatore, Madras; Coonoor, 1500 m; Madras St, Trichinopoly; Madras St, 12·9 km S. of Yercand; Tinevelly distr., Dohnavur; Coimbatore distr., Siruvani, 510 m, Coimbatore distr., Bolampatti valley; Coimbatore distr., Walayar; Hasanur, Biligirirangan Hills; Alagar Kovil, Madura distr.; Nelliampatti Hills; Travancore, Kottayam; Travancore, Tenmalai, 150–240 m; Coonoor, 1800 m; Bihar, Bhagalpur; Biligirirangan Hills, Dhimban; W. Bengal, Maharajpur; Mysore St, Shimoga distr., Tuppur Forest; Punjab, Murree Hills, Tret; Simla Hills, 1500–2100 m; Punjab, Altoe, 600 m; Simla, 1050–1350 m; Punjab, Gurdaspur; Bengal, Dhub; Jubbalpore. **Sri Lanka:** Jaffna; Malla to Illupallama; Diyatalawa; Hambantota; Colombo; Man distr., Mannar I., 4·8 km NW. of Mannar. **Nepal:** Phewa Tal, nr Pokhara, 750 m; 6·4 km W. of Pokhara, 900 m; Talkot, 1800 m; Arun valley, Tumlingtar, 540–600 m. **Bangladesh:** Dacca. **Burma:** S. Shan states, Kalaw, 1350 m; Upper Burma, 25·8 km on Magwe road, 150 m; Upper Burma, Lashio. **China:** Hainan I., Wutoshi; Hainan I., You Boi; Yergand; Canton, Honan I.; 1 ♀, 'abruptus *β*', no data, (ZIUU, Uppsala) (paralectotype of *Gryllus abruptus* Thunberg). **Thailand:** Lop Buri; Udon Thani, 17°25′N, 102°45′E; Chiang Mai; Doi Chiang Dao N, 1200 m.

DISTRIBUTION (Fig. 157, and Biogeography section, p. 163). Widely distributed in mainland east Asia.

BIOLOGY. *O. abruptus* has at least two generations per year with eggs overwintering from November to April. These hatch to give adults June–July which lay eggs, giving a second generation of adults in August–September (Ahmed *et al.*, 1973). The egg pod is short and fragile, laid in hard soil to a depth of 25–35 mm. There are 18–27 eggs per pod, each about 3·15–4·15 mm long and 0·85–0·95 mm across (Katiyar, 1960). In the laboratory maximum survival rates and fastest development occurred at 35°C and 8·0% humidity (Khan & Aziz, 1974). Maturation was slower and survival lower in crowded compared to solitary conditions (Khan & Aziz, 1976). The chromosomes have been studied by Asana *et al.* (1939), Dutt (1952; 1955), and Manna (1954). The species is a suitable experimental intermediate host of cestodes parasitic in crows and domestic fowl (Dutt & Sinha, 1961; Dutt & Mehra, 1962). The egg parasite *Scelio aegyptiacus* has been reared from eggs of *O. abruptus* in the laboratory (Ahmed *et al.,* 1973). There are a number of reports of crop damage. Ballard (1921) recorded damage to *Eleusine,* and Chopard & Chatterjee (1937) reported attacks on *Pinus* and *Shorea* seedlings and sandal. *O. abruptus* has also been found on maize and rice (Roffey, 1964; 1965), and is said to feed also on wheat, bajra, jowar, tomato, grain pea, groundnut and other crops (Khan & Aziz, 1974).

DISCUSSION. The measurements above indicate that specimens from Hainan are larger with relatively longer tegmina and a larger ratio of femur length to depth than those from Sri Lanka which is the southern limit for this species. It would be of interest to compare these populations with samples from Nepal on the north-west limit of its range. Thunberg's type-material of *Gryllus abruptus* comprises one male, here designated lectotype, and one female, designated paralectotype.

Oedaleus virgula (Snellen van Vollenhoven, 1869)
(Figs 24, 42, 79–82, 162)

Oedipoda virgula Snellen van Vollenhoven, 1869: 11. Holotype ♀ [not ♂ as stated by Snellen van Vollenhoven, op. cit.], MADAGASCAR (RNH, Leiden) [examined].

Epacromia inclyta Walker, 1870: 773. Holotype ♀, MADAGASCAR (BMNH) [examined]. [Synonymized by Uvarov, 1925: 276.]

Oedaleus (*Gastrimargus*) *madecassus* Saussure, 1884: 115. LECTOTYPE ♀, MADAGASCAR (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1925: 276.]

Oedaleus (*Oedaleus*) *nigro-fasciatus* var. *virgula* (Snellen van Vollenhoven) Saussure, 1888: 40; Kirby, 1910: 226.

Oedaleus inclytus (Walker) Kirby, 1910: 226.

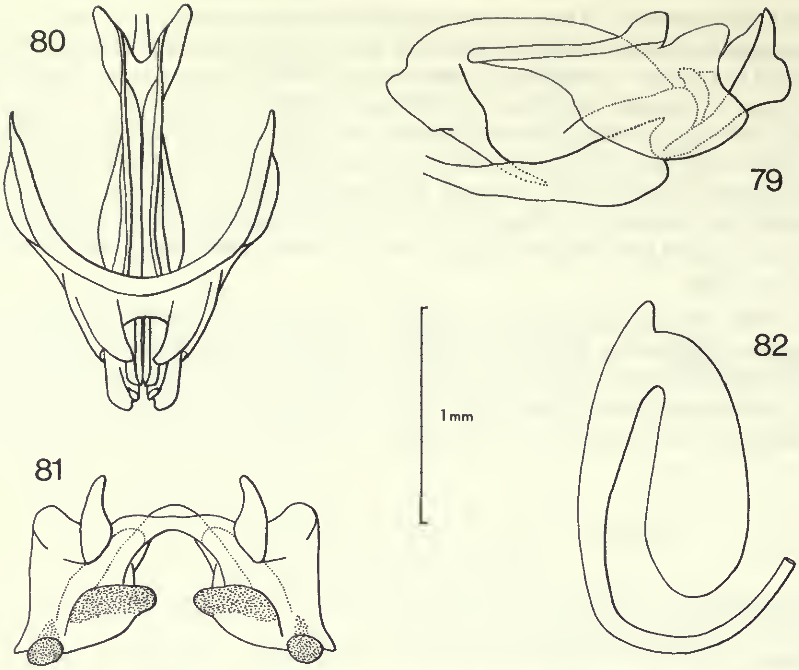
Oedaleus virgula (Snellen van Vollenhoven); Kirby, 1910: 226.

Oedaleus virgulus (Snellen van Vollenhoven); Dirsh, 1961*b*: 398. [Unjustified emendation.]

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a quarter to one and a third times as long as head and pronotum together; flagellum with 22–24 segments. Fastigium of vertex wider than long, anterior width one-third of maximum width, concave with raised margins; frons in profile straight to slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases, becoming obsolete ventrally. Eyes nearly one and a half times as deep as wide. Pronotum tectiform, finely punctate; median carina shallowly arcuate, hind margin acutangular to obtusangular. Tegmen surpassing hind knees by two-fifths to one-half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer, apical tarsal segment twice length of claw, arolium more than half claw length. Cerci about two and a quarter times as long as basal width. Genitalia (Figs 79–81): cingular apodemes slender, rami moderate length; cingular and apical penis valves short; subapical ventral process large; epiphallus almost rectangular with thin bridge; inner lobes of lophi strongly transverse, two and a half times as wide as outer lobes; anterior projections large, rounded; posterior projections small, sharply acutangular.

General coloration variable, greenish or brownish, with lighter markings on frons, genae, pronotum, tegmina and hind femora. Pronotal X-marking (Fig. 24) sometimes obsolescent. Tegmen infuscate in basal half with four pale transverse bands extending from costal margin; first band one-sixth along from base, reaching second cubitus, second band one-third along, reaching first or second cubitus, third band reaching and following *Cu1b* as a distinct oblique white stripe; fourth band two-thirds along, reaching posterior medial vein; apical third of wing mottled with brown and transparent cells. Hind wing without fascia or with very pale indistinct fascia barely visible posterior to second anal vein; basal area pale yellow. Hind femur with three variable transverse dark markings on external and internal upper marginal areas, extending obliquely across external and internal medial areas, sometimes obsolescent; ventral surface of femur straw-coloured, hind knee brown. Hind tibia with dark basal ring, subbasal pale area, otherwise pale blue-grey.

♀. Ventral ovipositor valves (Fig. 42) blunt, heavily sclerotized, exterior lateral surface almost straight; basivalvular sclerite coarsely rugose. Spermatheca (Fig. 82) with apical diverticulum elongate and short blunt sub-apical diverticulum.



Figs 79–82 *O. virgula,* genitalia. 79, endophallus and cingulum, lateral view; 80, same, dorsal view; 81, epiphallus; 82, spermatheca.

MEASUREMENTS
Sample from Madagascar: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·87	3·43	4·33	19·39	12·53	2·97	4·22	4·48
Range	22·1– 28·7	3·2– 3·8	3·6– 5·0	16·4– 21·5	11·1– 13·9	2·6– 3·2	3·9– 4·5	4·0– 4·8
S.D.	1·829	0·139	0·354	1·512	0·732	0·141	0·182	0·190
n	21	21	21	21	17	17	17	21

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	34·58	4·77	5·90	25·89	16·0	3·84	4·18	4·4
Range	29·7– 38·4	4·3– 5·2	4·9– 7·0	21·8– 28·9	14·1– 18·3	2·7– 4·5	3·8– 5·1	3·9– 4·7
S.D.	2·624	0·249	0·476	1·978	1·226	0·307	0·255	0·225
n	33	31	34	34	32	31	31	33

AFFINITIES. *O. virgula* belongs to the same species-group as *O. senegalensis* and *O. nigrofasciatus* on the basis of the pale hind tibia and underside of the hind femur, and the close similarity of the genitalia, particularly the epiphallus (Fig. 81). It is, however, easily distinguished from all the other species of the group by the absence of a distinct wing band.

MATERIAL EXAMINED

Oedipoda virgula Snellen van Vollenhoven, holotype ♂, **Madagascar:** no further data (RNH, Leiden). *Oedaleus* (*Gastrimargus*) *madecassus* Saussure, lectotype ♀, **Madagascar:** no further data (MHN, Geneva). *Epacromia inclyta* Walker, holotype ♀, **Madagascar:** no further data.

Madagascar: 1 ♂, 2 ♀, no further data; 1 ♀, Majunga s. 1., 25.ii–3.iii.1968 (*Guichard*); 1 ♂, 4 ♀, Glorieuses Is., 21.xi.1952 (*Brown*); 2 ♀, Ejeda, Betioky, Tulear, 27.i.1928 (*Zolotarevsky*); 1 ♂, 3 ♀, same data, 1.ii.1928; 3 ♀, same data, 21.ii.1928; 5 ♀, same data, 16.ii.1928; 2 ♀, same data, 5.v.1928; 1 ♂, 2 ♀, Sakamena, Betioky, 15.v.1928 (*Zolotarevsky*); 4 ♀, Ankazoabo, Tulear, 7.vi.1927 (*Zolotarevsky*) 1 ♂, Namsana, Tananarive, 18.ix.1928 (*Zolotarevsky*); 3 ♀, Ankililoaka, Tulear, 26.v.1927 (*Zolotarevsky*); 1 ♂, Nossi Bé, xi.1952 (*Brown*); 1 ♂, Ambohimandry, 30.viii.1913 (*Beck*); 1 ♀, Tsiafakomba, Adriba Isibefe (*Beck*); 5 ♂, 3 ♀, Antanemora, 300 m, xi–xii.1959 (*Ross*) (CAS, San Francisco); 3 ♂, 4 ♀, Zombitsy forest, nr Sakaraha, 650 m, 16.xii.1959 (*Ross*) (CAS, San Francisco); 1 ♂, 1 ♀, Tananarive, 5.xii.1959 (*Ross*) (CAS, San Francisco); 8 ♂, 1 ♀, same data, x.1949 (CAS, San Francisco); 2 ♂, Amboasary, Ft Dauphin dist., 18.iv.1969 (*Hardy*) (DATS, Pretoria); 2 ♂, 1 ♀, Tananarive, iii.1918 (*Lamberton*) (ANS, Philadelphia); 1 ♀, same data, ii.1918 (ANS, Philadelphia); 1 ♀, Behanka, Betioky, Tulear, 27.i.1928 (*Zolotarevsky*). **Aldabra:** 1 ♂, 1 ♀, Ans Mais, 22.iv.1977 (*Waloff*) (COPR, London). **Zanzibar:** 1 ♀, no data (*Hildebrandt*) (MNHU, Berlin). **South Africa:** 1 ♀, Cape of Good Hope, 1820 (*Delalande*) (MNHN, Paris) [almost certainly mislabelled].

DISTRIBUTION (Fig. 162, and Biogeography section, p. 163). Widely distributed and common within Madagascar, and newly recorded from Zanzibar and Aldabra. There is one specimen purporting to be from South Africa, but this is presumably mislabelled.

BIOLOGY. Little is known of the biology of this species. The following information is derived from Descamps & Wintrebert (1966). One egg pod was measured and found to be 57·5 × 5·0 mm, slightly bent, with 30 eggs arranged in 11 rows of 2–4 eggs each. The individual eggs are about 4·1 × 1·0 mm and have a chorionic sculpture composed of irregular dots forming indistinct rows, with neighbouring dots sometimes joined by fine lines. In the cool season incubation lasts at least two months. The sixth instar may last a month. Nymphs are particularly common in September, November, March, and April. There are three or possibly four generations per year with an apparent movement of adults southward at the end of the hot season. Three species of *Scelio* were recorded as egg parasites.

DISCUSSION. The emendation of the specific name *virgula* to *virgulus* (Dirsh, 1961*b*) is here rejected because *virgula,* meaning a wand, is a feminine noun in apposition and not an adjective.

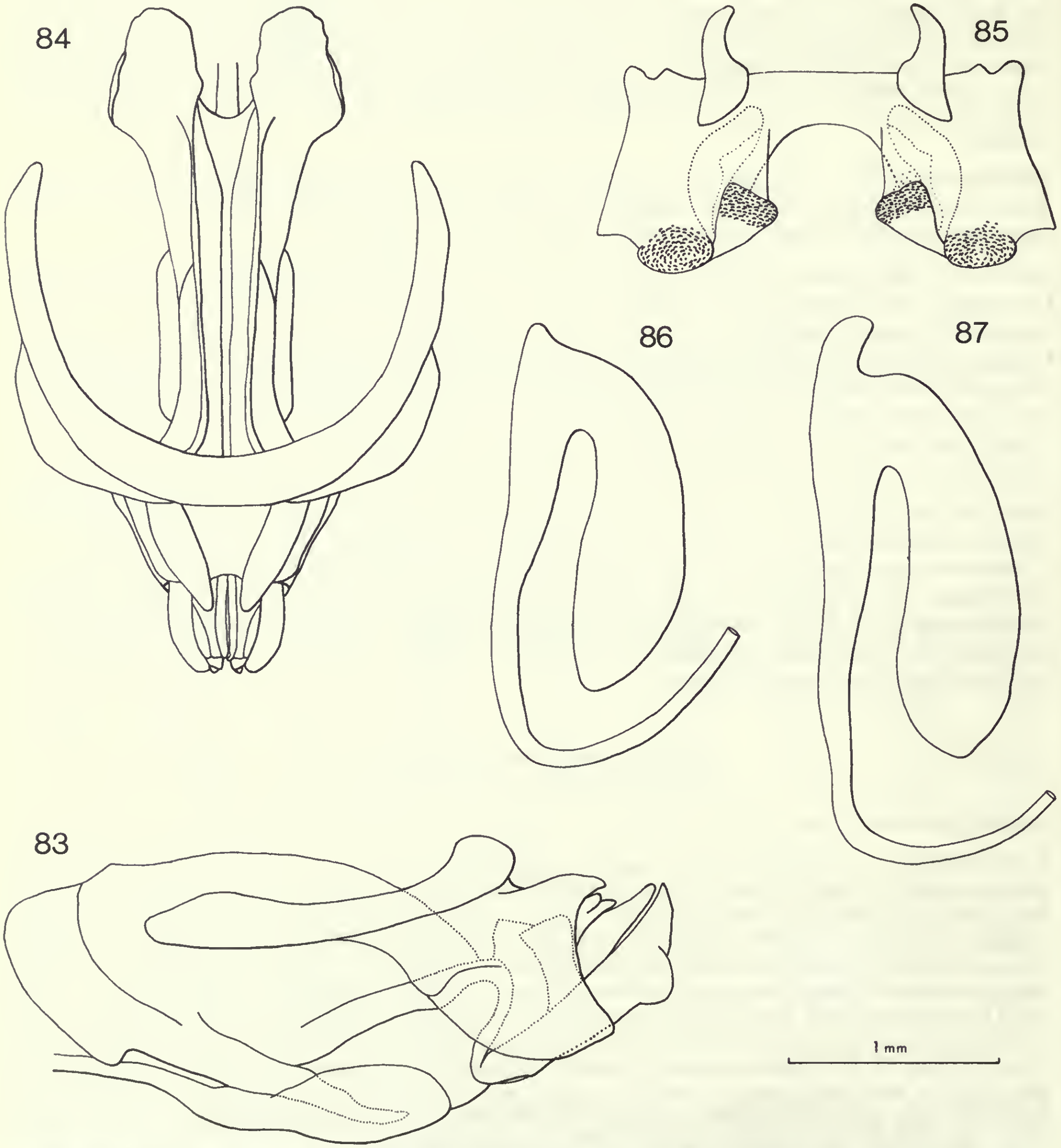
Saussure's description of *O. madecassus* was based on material in his own and Brunner's collections. The single male of this species in the MHN, Geneva, bears the following labels: 'Madagascar M. H. de S.' '*Oedaleus madecassus* Sss. Madag.'. This specimen is here designated as the lectotype. The status of material in the NM, Vienna, is not clear and accordingly no paralectotypes have been designated.

Oedaleus johnstoni Uvarov, 1941
(Figs 14, 19, 43, 83–87, 155)

Oedaleus johnstoni Uvarov, 1941: 58. Holotype ♂, SUDAN: Khartoum (BMNH) [examined].

REDESCRIPTION. ♂. Integument finely rugulose. Antennae about one and two-fifths length of head and pronotum together; flagellum usually 22-segmented. Fastigium wider than long, concave, with raised margins, narrowing to half maximum width anteriorly. Frons in profile flat or slightly convex; frontal ridge slightly expanded at ocellus. Eyes barely deeper than wide. Pronotum low tectiform to saddle-shaped, finely rugulose, pitted, and with well-marked sulci; median carina low and cut by posterior sulcus. Hind margin of pronotum smoothly rounded. Tegmen surpassing hind knees by about one-third of femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times as long as claw; arolium about one-third length of claw. Cerci almost twice as long as basal width. Genitalia (Figs 83–85): cingular apodemes long and strongly curved, zygoma only slightly thickened; rami long; cingular and apical penis valves short. Apical penis valves with acute apices and tumulus-shaped subapical ventral process. Epiphallus long and broad with deeply arched bridge; outer lobes of lophi wider than inner lobes; anterior and posterior projections large and acutangular.

General coloration mottled, variable, from dark brown to sandy or greenish. Head mainly light brown, sometimes with frons and vertex green. Lateral surface of pronotum and thorax mottled with variable light and dark patches. Pronotum sometimes entirely green on dorsum of prozona and metazona but laterally on metazona only. Tegmen mottled with two indistinct variable transverse bands in basal two-thirds, apex with some dark speckling. Hind wing fascia (Fig. 14) incomplete, not reaching posterior margin and not passing *2A* anteriorly; basal area pale yellow. Outer surface of hind femur with three indistinct oblique dark bands, inner surface with some bands visible in upper-marginal area but medial area clear straw-coloured, with orange sulci in chevron pattern, lower marginal area bright orange. Hind knees with internal surface and external crescent black. Hind tibia bright orange internally, orange-yellow externally.



Figs 83–87 *O. johnstoni,* genitalia. 83, endophallus and cingulum, lateral view; 84, same, dorsal view; 85, epiphallus; 86, 87, spermatheca, showing variation.

♀. Pronotum more rugose. Ventral ovipositor valves (Fig. 43) barely longer than wide, slightly excavated laterally; basivalvular sclerite sclerotized and with rugose warts. Spermatheca (Figs 86, 87) elongate with short, variable subapical diverticulum.

MEASUREMENTS
Sample from Mali: Adrar des Iforhas.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur width	FL/FD	TL/PL
Mean	30·18	4·88	4·87	21·90	13·80	3·88	3·74	4·56
Range	26·3–	4·5–	4·2–	18·4–	12·6–	3·1–	3·5–	3·9—
	35·4	5·3	5·6	25·9	17·3	4·4	4·2	5·3
S.D.	2·267	0·223	0·357	1·864	3·126	0·384	0·211	0·373
n	14	19	19	14	19	19	19	14

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur width	FL/FD	TL/PL
Mean	40·09	6·67	6·38	29·03	18·58	4·79	3·89	4·55
Range	36·75–	6·1–	5·5–	26·0–	17·0–	4·1–	3·6–	4·0
	45·5	7·6	7·7	32·8	21·0	5·7	4·2	4·8
S.D.	2·69	0·425	0·633	1·934	1·269	0·474	0·188	0·23
n	20	20	21	20	21	21	21	20

AFFINITIES. *O. johnstoni* is most closely allied to *O. senegalensis* and *O. nigeriensis,* having the rounded pronotal hind margin of the former and the orange-red hind tibiae and under surface of the hind femur reminiscent of the latter. It is, however, quite distinct, being more heavily built and having a lighter, less distinct pattern than either of these species.

MATERIAL EXAMINED

Oedaleus johnstoni Uvarov, holotype ♂, **Sudan:** Khartoum, 25.ix.1924 (*Johnston*) (BMNH).

Mauritania: 5 ♂, 4 ♀, 17° 12′N, 13°58′W, light trap, 19.ix.1973 (*Popov*); 2 ♂, 1 ♀, Aioun, 16°40′N, 9°31′W, 10.x.1961 (*Popov*). **Mali:** 4 ♂, 2 ♀, Adrar Mts, nr Tabankort, 7.ix.1959 (*Popov*); 1 ♀, Pèhé, 40 km N. of Dioura, 16.x.1956 (*Davey*); 2 ♂, 1 ♀, Tillemsi Valley, road from Kidal to Tin-Essakou, 29.ix.1974 (*Ritchie*) (COPR, London); 17 ♂, 20 ♀, Adrar de Iforhas, Oued Edjerer, 30.ix.1974 (*Ritchie*) (COPR, London). **Niger:** 1 ♂, 30 km E. of Agadez, 20.ix.1965 (*Popov*); 1 ♀, Gall-Abangharit, 10.xii.1960 (*Popov*); 2 ♂, 5 ♀, Abangharit, 12–19.ix.1965 (Popov); 1 ♀, Aïr, 100 km N. of Agadez towards In Guezzam, 25.viii.1967. **Sudan:** 4 ♂, 1 ♀, Khartoum, 25.ix.1924 (*Johnston*) (paratypes of *Oedaleus johnstoni* Uvarov); 1 ♀, Khartoum (*King*) (paratype of *O. johnstoni*); 3 ♂, 1 ♀, Khartoum, 20.ix.1970, 1 ♂, 4 ♀, Kassala, 3.x.1926 (*Johnston*) (paratypes of *O. johnstoni*); 5 ♀, Aroma, short grass, 30.ix.1926 (*Johnston*) (paratypes of *O. johnstoni*); 1 ♂, 4 ♀, Aroma, dry grass, 3.x.1926 (*Johnston*) (paratypes of *O. johnstoni*); 1 ♂, 4 ♀, no further data (paratypes of *O. johnstoni*); 6 ♂, N. Darfur, clay wadi, at light, 9.ix.1934 (*Darling*); 1 ♀, N. Darfur, Jebel Jeiga, 24.ix.1934 (*Darling*); 1 ♀, Wad Medani, at light, ix.1927 (*Johnston*); 1 ♀, Barakat, 10.x.1974 (*Haggis*) (COPR, London); 1 ♀, Barakat, 14.x.1974 (*Haggis*) (COPR, London). **Ethiopia:** 1 ♂, Harerge pr., Melka Werer, Inst. Agr. Res., 14·5 km ENE. of station, 30.ix.1975 (*Jago*) (MA, Addis Ababa). **Oman:** 1 ♂, Al Khaburah, 22.x.1970 (*Tunstall*) (COPR, London).

DISTRIBUTION (Fig. 155, and Biogeography section, p. 162). Occurs in a thin band across the northern Sahel from Mauritania to Ethiopia (Jago, 1977), and there is one known specimen from Oman, a new record which needs confirmation. An erroneous record from Senegal by Roy (1962: 130) was later identified as *Oedaleus nigeriensis* Uvarov (Roy, 1965: 616).

BIOLOGY. Little is known of the biology of this species. Joyce (1952) recorded it from sandstone and serpentine outcrops in east-central Sudan, and regarded it as the dominant species in sandy areas of the Gash river delta (200–300 mm annual rainfall) and the clay plains of the northern Gezira (150–200 mm rainfall). Adults were found from August to November with peak numbers in August and September. Hoppers occurred between July and October and mature females from August. Joyce postulated two annual generations, with the dry season passed in the egg stage in dry soils. There are records of damage to millet (Joyce, 1952) and to cotton (Joyce, 1956) but such damage is probably rare and of small extent.

O. johnstoni normally occurs in low densities but very high density populations have been reported. Dr R. Skaf (pers. comm.) observed bands of fourth and fifth instar hoppers at a density of 100/m^2 marching westward downwind in the Oued Edjerer (18°26′N 02°02′E) in NE. Mali on 20.viii.1974. The hoppers collected exhibited pronounced black and brown coloration like that of high density hoppers of *O. senegalensis*, and small numbers of adult *O. senegalensis* were mixed among them. On 30.ix.1974 I visited the locality and found adults only at about 1 per 2–3 m^2. The decline in numbers over five weeks may be attributed to dispersal of adults by flight since the species is often caught at light some distance from areas where it can be found by day. *O. johnstoni* is the dominant grasshopper species in the flat, gravelly silt oueds flowing into the Tillemsi valley from the rocky outcrops of the Adrar des Iforhas, and its coloration is well matched to that of the extensive patches of bare soil on which it rests. The sparse vegetation consists of low hummocks of *Tribulus, Euphorbia, Indigofera, Farsetia,* and *Heliotropium* with *Aristida* and *Panicum turgidum*. The insects fly readily when first disturbed but land and hide within the clumps of vegetation and are then difficult to flush a second time.

Adult specimens possess a pronotal gland similar to that found in *O. senegalensis* but no hoppers were available for dissection. The ovaries of seven adult females were dissected and the mean number of ovarioles per ovary was found to be 26·8 with a range from 23 to 31.

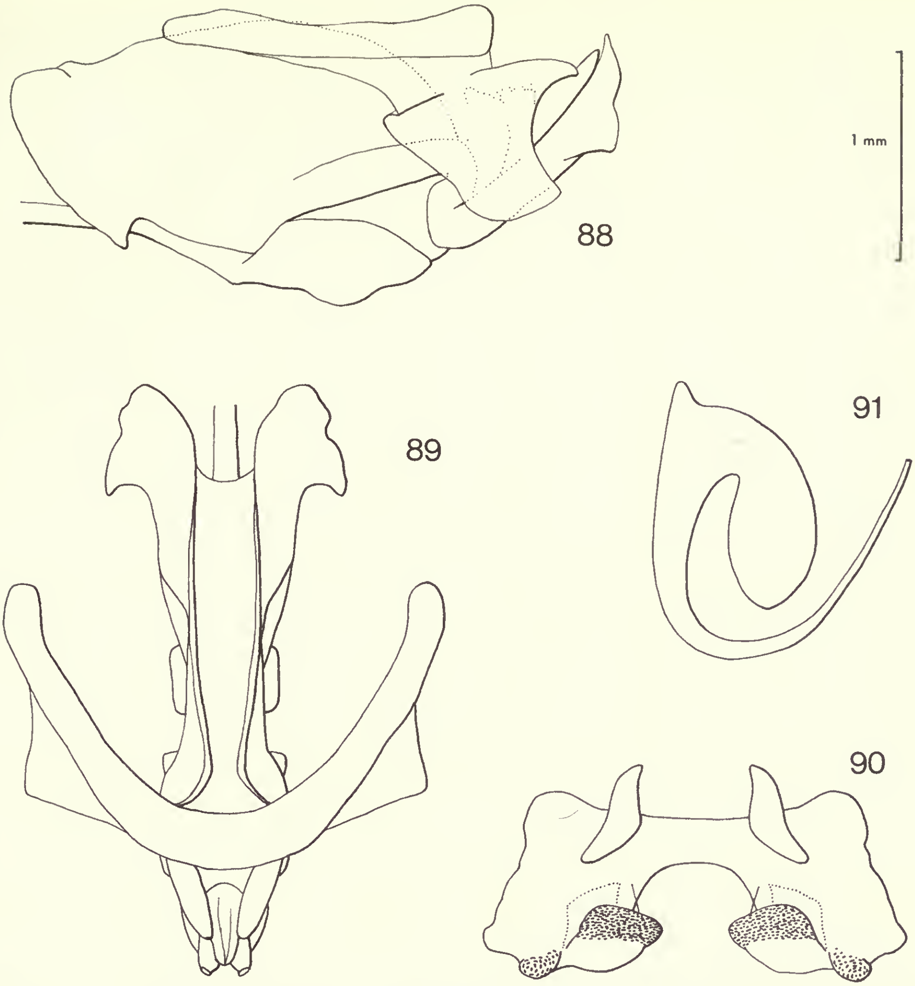
Oedaleus nigeriensis Uvarov, 1926
(Figs 10, 20, 39, 88–91, 161)

Oedaleus nigeriensis Uvarov, 1926: 437. Holotype ♂, NIGERIA (BMNH) [examined].
Oedaleus senegalensis (Krauss) var. *b.* Saussure, 1884: 117; Bolivar, 1908: 102.
Oedaleus cephalotes Uvarov, 1934: 606. Holotype ♀, ETHIOPIA (BMNH) [examined]. **Syn. n.**

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and three-fifths times as long as head and pronotum together, flagellum with twenty segments. Fastigium longer than wide, shallowly concave, narrowing to two-fifths of maximum width anteriorly; frons in profile convex; frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and two-fifths as deep as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular to rounded obtusangular. Tegmen surpassing folded hind knees by two-fifths to one-half of hind femur length. Hind tibia with 10–11 inner and 8–10 outer spines; inner apical spurs one and three-fifths as long as outer; apical tarsal segment two and one-fifth times as long as claw; arolium three-fifths length of claw. Cerci barely more than twice as long as basal width. Genitalia (Figs 88–90): cingular apodemes short and moderately curved; rami elongate dorsally; exposed section of cingular and apical penis valves short; subapical ventral process rectangular; epiphallus trapezoidal, bridge narrow; inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal two-thirds with irregular pale transverse bands one-third and one-half along from base; apical one-third clear with variable brown patches. Hind wing fascia (Fig. 10) broadly interrupted between first cubitus and second anal vein, reaching or nearly reaching to hind margin posteriorly; wing tip infumate, basal area pale yellow. Hind femur with three indistinct dark variable oblique transverse bands on outer and inner upper marginal areas and outer medial area; inner surface light reddish brown becoming pale red ventrally; hind knees dark brown; hind tibiae with dark basal ring and subbasal pale area, otherwise light red.

♀. Ventral ovipositor valves (Fig. 39) long, well sclerotized, outer margin almost straight. Apical diverticulum of spermatheca (Fig. 91) with short subapical diverticulum.



Figs 88–91 *O. nigeriensis*, genitalia. 88, endophallus and cingulum, lateral view; 89, same, dorsal view; 90, epiphallus; 91, spermatheca.

MEASUREMENTS

Sample from Zambia: Musosa, xi–xii.40 [beginning of rainy season] (*H. J. Bredo*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·99	3·33	3·725	17·75	11·44	2·87	3·98	4·73
Range	22·1– 25·8	3·1– 3·7	3·3– 4·1	16·7– 18·7	10·4– 12·6	2·7– 3·0	3·6– 4·4	4·3– 5·3
S.D.	0·999	0·152	0·216	0·661	0·661	0·071	0·200	0·222
n	16	17	16	16	17	17	17	15

Females

Mean	29·99	4·47	4·78	22·22	13·96	3·64	3·83	4·66
Range	26·5–	3·9–	4·2–	19·6–	12·0–	3·1–	3·6–	4·2–
	33·5–	5·0	5·3	25·5	15·4	4·0	4·1	5·2
S.D.	1·558	0·223	0·275	1·331	0·819	0·165	0·128	0·235
n	20	20	20	20	20	20	20	20

Sample from Zambia: Musosa, iv–v.41 [end of rainy season] (*H. J. Bredo*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	29·05	4·33	4·57	21·36	14·82	3·39	4·37	4·69
Range	27·0–	4·1–	4·2–	20·1–	14·4–	3·0–	4·1–	4·2–
	30·4	4·7	5·1	22·4	15·5	3·7	4·7	5·1
S.D.	1·051	0·186	0·261	0·790	0·530	0·204	0·172	0·231
n	10	10	10	10	9	10	9	10

Females

Mean	36·49	5·78	5·71	26·57	18·42	4·31	4·28	4·67
Range	34·7–	3·5–	5·2–	25·4–	16·8–	4·2–	4·0–	4·4–
	37·8	6·2	6·2	27·8	20·2	4·5	4·8	5·0
S.D.	1·286	0·239	0·417	0·896	1·323	0·134	0·313	0·22
n	5	5	5	5	5	5	5	5

Sample from Ethiopia: Nefasit, 28.viii.68 (*J. Tunstall*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·62	3·72	3·9	17·04	12·54	3·14	3·99	4·38
Range	22·3–	3·4–	3·6–	16·1–	11·5–	2·9–	3·7–	3·9–
	26·1	4·2	4·3	19·1	13·5	3·4	4·2	4·70
S.D.	1·267	0·210	0·227	0·937	0·592	0·148	0·156	0·22
n	11	11	11	11	11	11	11	11

Females

Mean	32·24	5·36	5·24	22·66	16·69	4·07	4·1	4·33
Range	28·9–	4·8–	4·5–	20·8–	14·4–	3·6–	3·8–	4·1–
	35·9	5·7	5·8	24·9	19·1	4·4	4·4	4·7
S.D.	1·905	0·279	0·369	1·088	1·141	0·224	0·177	0·176
n	12	12	12	12	12	12	12	12

AFFINITIES. *O. nigeriensis* is a member of the same group of species as *O. senegalensis*, characterized by the possession of large transverse inner lobes to the epiphallic lophi. It is most closely allied to *O. carvalhoi* from which it may be separated by the principal characters listed under that species (p. 117).

MATERIAL EXAMINED

Oedaleus nigeriensis Uvarov, holotype ♂, **Nigeria:** Azare, vii.1925 (*Lloyd*) (BMNH). *Oedaleus cephalotes* Uvarov, holotype ♀, **Ethiopia:** Muger Valley, c. 5500′ [1600 m], 28–29.xii.1926 (*Scott*) (BMNH).

In addition to the holotypes, 787 specimens were examined from the following localities. **Senegal:** Bambey; Dakar; Dakar, Cape Manuel; Yoff; Mt Rolland; Diebering; Thies. **Mauritania:** Néma; Selibaby area. **Mali:** Bamako; Kara, Macina; Sangha Village; 2·4 km E. of Sangha; Klela; Gourima, nr Darou; Dogo; Nioudji. **Upper Volta:** Ouagadougou. **Ghana:** Volta Region, Nkwanta to Chiare; N. region, 8 km S. of Lepusi, 51·5 km S. of Yendi; Nakpanduri, Gambaga Scarp; Navrongo; N. region, Damongo. **Togo:** Mangu; Kete Kratje. **Niger:** Niamey to Tillabery, 35 km from Niamey; Elewayen, agric. station; Danga village, nr Ouallam. **Nigeria:** 2 ♂, 1 ♀, Azare, vii.1925 (*Lloyd*) (paratypes of *Oedaleus nigeriensis* Uvarov); Ibadan, Ife University campus; Kalkala; Ngornu, Bornu; Potiskum; Sherifuri, nr Azare; Ngala; Kerenua; Maiduguri; Dikwa; Shagisnu; Wurge; Birnin Kudu; Maiduguri to Bama road; km 35–37, Mongonu to Maiduguri road; 8·9 km W. of Gulumba; 2·5 km N. of Debele village; Lamurde hills; Zaria; Zaria, Samaru; 50 km S. of Bama; 45 km SE. of Maiduguri; Bauchi, air strip; Maska, fish farm; nr Yola; 96·6 km along Kaduna to Tegina road; Shika, I.A.R. farm; nr Difa, Gombe area; nr Deba Habe; Zambuk, nr Gombe; nr Bilbis turn-off, on Zaria to Chafe road. **Cameroon:** Gore; Kuni; Kaitia; Sogane to Gore; Middle Adamaua, 300–500 m, v. Garua und Rei Buba, n. Monti; Garua; Satsche. **Congo:** environs of Brazzaville. **Central African Empire:** Batangafo, Ubangi to Shari. **Zaire:** Mahagi Port; Kawa, L. Albert; Ekibondo, between Niangara and Dungu, Uele, 795 m; Kasenyi, L. Albert, 630 m. **Angola:** E. region; Moxico distr., Villa Luzo, 900 m; Moxico Pr., Villa Luzo; Moxico distr., R. Lumeji; 8 km NE. of Negola. **Zambia:** Lusaka distr.; Lusaka distr., nr Kipopo; Ndola; Livingstone; 30 km outside Kitwe; Musosa. **Tanzania:** Kondoa; Old Shinyanga; Ushirombo road, 16 km W. of Kahama; Mkwemi, 35·4 km W. of Kahama; Central Rukwa, side of W. escarpment; C. Rukwa, Kapombo; C. Rukwa, Kafukola; Nakachese, Rukwa rift; Momba R., Rukwa rift. **Uganda:** Butiaba, L. Albert, Unyoro, 624 m; Lango, Kigaa (Agaya); Lango; Bugwere; W. Nile distr.; Dokolo; Moroto; Karamoja, Kotido; S. Karamoja, Madi Opei; Soroti; Teso; Adachal; Butiaba; Kamuli, Busoga; Bukumi, L. Albert; Sukh plains, nr Nepal Pass; Buruli; Chiawante, Lango; Mbale. **Kenya:** Kindaruma, 3·2 km N. of bridge across Tana R., 00°47·5′S, 37°39·5′E, 1070 m; Makindu; 41 km N. of Kitui, 01°08·5′S, 37°44′E; Athi R. crossing, 25·8 km NNE. of Kibwezi, 420 m; Sumba Springs; Murinduko hill (top), 4·8 km S. of Embu town, 00°35′S, 37°27′E, 1300 m, game area owned by Taita Hills Lodges, 03°32′S, 38°14′E, 900 m; Kitito Coffee Estate, 00°58′S, 37°17′E, 1560 m. **Sudan:** Imatong Mts, Lorno, 810 m; Imatong Mts, Molongori, 750 m; Bahr el Ghazal, 16 km W. of Rumbeck, on Wau to Rumbeck Road; Opari; Talodi; Gedaref, M.C.P.S.; Kerrippi. **Ethiopia:** Nefasit; Batie; Harar; Macalle; Addis Ababa to Debra Marcos road, Abbai gorge, about 2100 m; Eritraea, Elabaret; 1 ♀, plains NW. of L. Zwai, 1650–1950 km, 31.x.–1.xi.1926 (*Scott*) (paratype of *Oedaleus cephalotes* Uvarov); 1 ♂, no data (paratype of *O. cephalotes* Uvarov); Shewa Province, Mojo to Shashamene road, km 104·7, L. Shala bird sanctuary; 1 ♀, Wambar Mariam, Mt Zuquala, 2100 m, 28.x.1926 (*Scott*) (paratype of *O. cephalotes* Uvarov); Tembine distr., Avergalle area. **Comoro Is.:** 1 ♂, Grand Comoro, coast, 3.vii.1903 (*Voeltzkow*) (MNHU, Berlin).

DISTRIBUTION (Fig. 161, and Biogeography section, p. 163). Widely distributed in moist savannah and woodland from Senegal to Ethiopia and southwards through central Africa to the southern limits of the *Brachystegia* woodland. Newly recorded from Grand Comoro I.

BIOLOGY. The life history and ecology of *O. nigeriensis* were studied in Nigeria by Golding (1948) who stated that there were probably three generations in the south but only one in the north. In West Africa as a whole adults are to be found from April through to January. In Tanzania Robertson & Chapman (1962) made an ecological study which suggested that there were two generations between January and July, but they were unable to decide whether the species survived the dry season in the egg or adult stage, or in both. They presented evidence suggesting that young adults leave the grasslands and enter the woodland to feed or oviposit. In Cameroon Descamps (1953) postulated two generations with an embryonic diapause. The egg pod and eggs have been described by Chapman & Robertson (1958) who found 12–42 eggs per pod. The species has been recorded damaging maize (Descamps, 1954; Mallamaire, 1956), *Pennisetum* and *Eleusine* millet (Risbec, 1950; Golding, 1946; Libby, 1968; Harris, 1949), rice seedlings (Risbec & Mallamaire, 1949), groundnuts and sweet potato (Risbec, 1950) and tobacco and yams (Libby, 1968).

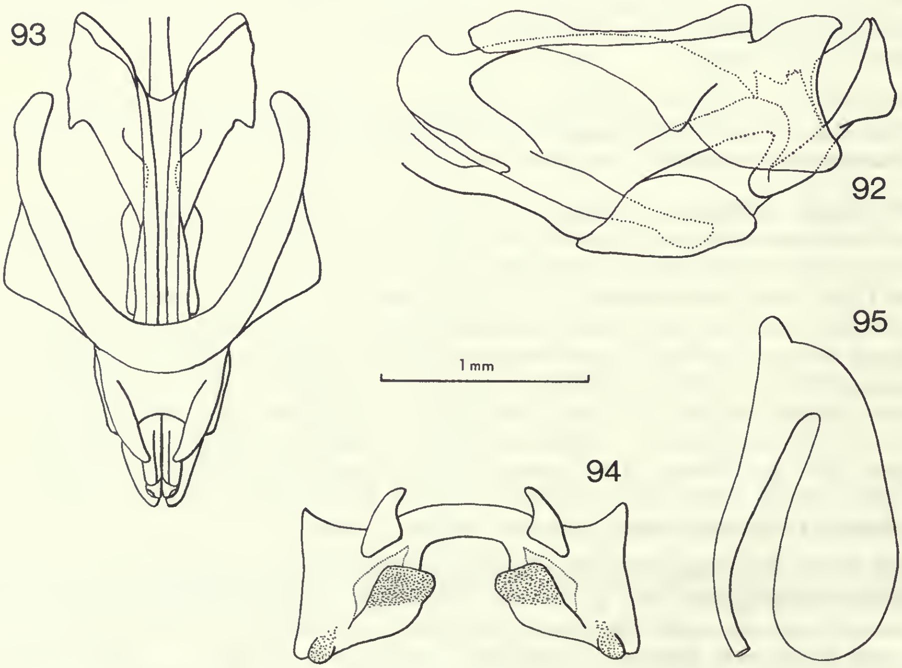
DISCUSSION. The measurements of specimens from Musosa, Zambia show the remarkable change in size exhibited by the species over six months. The ranges of measurements from the two samples barely overlap, and are clearly significantly different. Less obviously the ratio of femur length to depth is also significantly different as indicated by a 't' test ($P < 0{\cdot}001$ ♂, $< 0{\cdot}1$ ♀). It is not clear whether the two samples at either end of the rainy season represent two different generations of the same population or rather a migration into the locality of a population from elsewhere between the two sampling periods. For present purposes, however, these figures provide an indication of the range of size within the species. Series from Ethiopia and Tanzania fall within the extremes recorded from Zambia. Material from Ethiopia was originally named as a separate species, *O. cephalotes*, by Uvarov (1934) at a time when relatively little material of *O. nigeriensis* was known, and that only from Nigeria. It has now become clear that the same species is to be found without a break right across Africa. The original description of *O. cephalotes* made no comparison with material of previously described *Oedaleus* species.

Oedaleus carvalhoi Bolívar, 1889
(Figs 15, 23, 44, 92–95, 152)

Oedaleus carvalhoi Bolívar, 1889: 103. Syntypes (?) ♂♀, MOZAMBIQUE: Lourenço Marques [Maputo] (*Monteiro*) (lost). NEOTYPE ♂, MOZAMBIQUE (ANS, Philadelphia), here designated [examined].

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together, flagellum with 21 segments. Fastigium of vertex longer than wide, concave, narrowing to less than half of its maximum width anteriorly, with distinct lateral carinae; frons in profile straight, frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, not intersected by posterior sulcus; hind margin forming an obtuse angle with concave sides (Fig. 23). Tegmen surpassing hind knees by one-quarter to one-eighth of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times outer; apical tarsal segment one and three-quarter times claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 92–94): cingular apodemes long and incurved; rami elongate with short cingular and apical penis valves; subapical ventral process large, rounded; epiphallus rectangular with narrow bridge, inner lobes of lophi strongly transverse, more than twice width of outer lobes; anterior projections large, acute; posterior projections small, rounded.

General coloration variable, brown, with lighter brown or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina. Pale X-marking of pronotum often surrounded by longitudinal dark brown area. Tegmen matt brown in basal half with two irregular pale transverse bands one-third and one-half distance from base, sometimes obsolete; apical half becoming clear with irregular brown markings. Hind wing



Figs 92–95 *O. carvalhoi*, genitalia. 92, endophallus and cingulum, lateral view; 93, same, dorsal view; 94, epiphallus; 95, spermatheca.

fascia (Fig. 15) interrupted between first cubitus and second anal vein, reaching or almost reaching hind margin of wing; apex of wing infumate, basal area pale yellow. Hind femur with three indistinct variable oblique transverse dark bands on external medial and upper marginal areas; inner surface brown, indistinctly mottled, ventral surface dull brown; hind knees dark brown, hind tibiae with dark basal ring and pale subbasal area, otherwise dull brown.

♀. Hind wings sometimes barely exceeding folded hind knees. Ventral ovipositor valves short, well sclerotized, hardly incurved externo-laterally (Fig. 44). Spermatheca (Fig. 95) with short subapical diverticulum.

MEASUREMENTS

Sample from South Africa: Transvaal, Louis Trichardt.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·32	3·47	4·31	16·85	12·21	3·01	4·06	3·92
Range	21·5–	3·0–	3·9–	15·4–	10·3–	2·7–	3·7–	3·6–
	25·2	4·6	5·1	18·3	14·1	3·5	4·4	4·3
S.D.	1·131	0·333	0·301	0·864	0·948	0·199	0·211	0·181
n	20	20	20	20	20	20	20	20

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26·88	4·69	5·42	18·77	14·26	3·65	3·91	3·47
Range	24·8–	4·5–	5·1–	17·0–	13·5–	3·4–	3·6–	3·1–
	28·7	5·0	5·9	19·7	15·1	3·9	4·2	3·7
S.D.	1·032	0·139	0·204	0·781	0·482	0·149	0·173	0·172
n	15	15	15	15	15	15	15	15

AFFINITIES. *O. carvalhoi* is most closely allied to *O. nigeriensis* from which it differs by the following principal characters. Tibiae and ventral surface of hind femur pale straw-coloured, not red. Pronotum with finer cross-shaped marking and more pointed hind margin (Figs 23, 20). Tegmina and wings shorter in relation to body size and pronotum length (compare TL/PL ratios given for both species).

MATERIAL EXAMINED

Oedaleus carvalhoi Bolívar, neotype ♂, **Mozambique:** Lourenço Marques [Maputo], 12.vii.1910 (ANS, Philadelphia).

In addition to the neotype, 263 specimens were examined from the following localities. **Mozambique:** 35 km NE. of Chitengo, Gorongoza; 9·7 km E. of Vila Machado; Namaacha; 10 km E. of Marraguere; Missão de S. Roque, Maputo; Massinga; Zambezi R., Sena Sugar Estate; Beira, Milange; Beira, Luabo; Beira, Salone forest; Mucheve; Delagoa Bay, Inhaca I.; Buzi R.; Delagoa Bay. **Zambia:** Livingstone. **Zimbabwe:** West Nicholson, Masase; Dotts Drift, Chisumbanje, Lower Sabi; Mt Selinda, 1350 m; Bizana distr., Pondoland E.; 22·5 km NW. of Gwanda, Old Gwanda road, 1050 m; Shangani, de Beers Ranch; Matopo Hills; Odzi distr., Selukwe, 1500 m; Zimbabwe, nr Fort Victoria; Victoria Falls, 900 m. **Botswana:** Siane, Chobe. **Namibia:** Gobiswater Farm, 19·3 km N. of Grootfontein, 19°23′S, 18°08′E, c. 1400 m. **South Africa:** Transvaal, Zoutpansberg, 9·7 km NNE. of Louis Trichardt; T., Louis Trichardt; T., Wyllies Poort; T., Zoutpansberg distr., Limpopo R., along banks, nr Kobeehpan, 660 m; T., Tsaneen, 600 m; SW. Waterberg distr.; T., Zululand, Hluhluwe, 600 m; T., 6 km W. of Klaserie; T., 23 km S. of Brugersfort, 990 m; T., 24·2 km W. of Pongola, 550 m; T., 17·7 km N. of Louis Trichardt, 800 m; T., 3·2 km NE. of Boyne, 1150 m; T., Klaserie, 600 m; T., Maritzberg; T., Limpopo R., 23°00′S, 27°57′E, 840 m; T., 11·3 km W. of Potgietersrus, 24°17′S, 28°57′E, c. 1170 m; Natal, Durban, Umbilo; N., Pipetown; N., Amanzimtoti; N., Tugela R. Canyon, 30·6 km N. of Kranskop, 450 m; N., St Lucia, 50 m. **Swaziland:** Border post.

DISTRIBUTION (Fig. 152, and Biogeography section, p. 156). Widely distributed in the eastern half of southern Africa.

BIOLOGY. Little is known of the biology of this species. Nolte (1939), in his comparative study of seven species of Acrididae in the Transvaal, states that adult females have 18 ovarioles per ovary.

Adults were mainly found from October to April but sometimes in July and August. The species has a chromosome complement of 11 autosomes and an XO sex determination system. *O. carvalhoi* has been reported damaging cotton in Mozambique (Del Valle y Marche, 1968).

DISCUSSION. The type-material of *O. carvalhoi* Bolivar from Lourenço Marques was originally deposited at Lisbon. Dr J. de A. Fernandez kindly informs me that it is lost. In order to guarantee stability of nomenclature a neotype male is here designated from the original type-locality.

Oedaleus plenus (Walker)

(Figs 6, 22, 45, 96–99, 153)

Epacromia plena Walker, 1870: 769.

This species is divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugulose. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, narrowing to about three-quarters of maximum width anteriorly; lateral carinae distinct; frons in profile slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases. Eyes one and two-fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin from slightly acutangular to slightly obtusangular. Tegmen normal, surpassing hind knees by one-third to one-half of hind femur length. Hind tibia with 10 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and one-third times claw length; arolium three-fifths of claw length. Cerci little more than twice as long as basal width. Genitalia (Figs 96–98): cingular apodemes long, strongly curved; rami long; exposed portion of cingular valves and apical penis valves short, subapical ventral process rounded; anterior projections large, rounded; posterior projections rectangular.

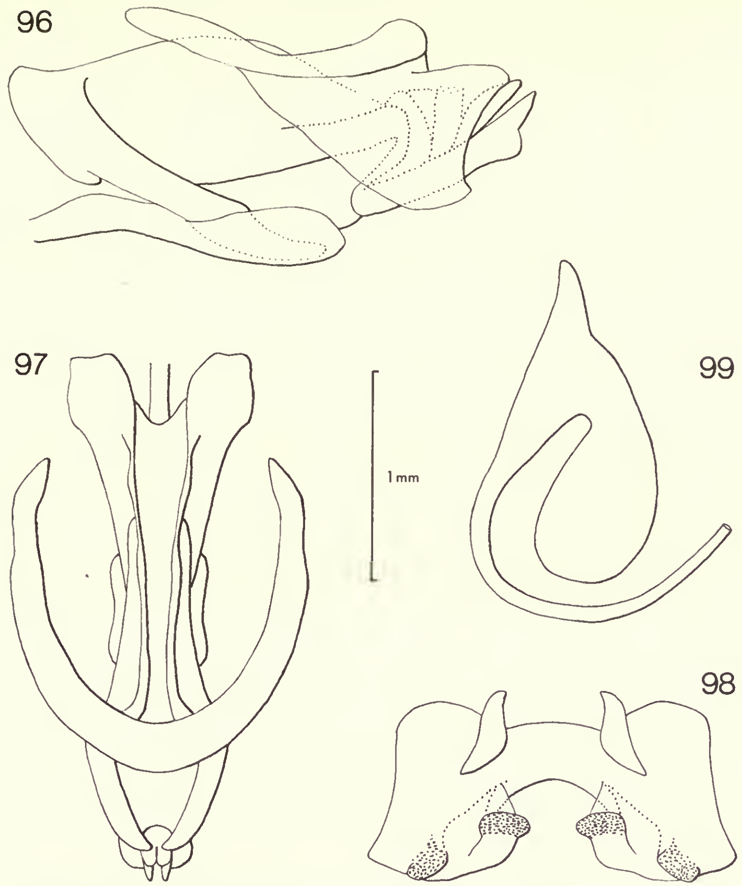
General coloration variable, brown, grey brown, or greenish; green forms rare, brown forms with lighter brown markings on frons, genae, and dorsal surface of pronotum, tegmen, and hind femur; green forms have green markings here and on vertex. Tegmen infuscate in basal half, with irregular pale transverse band one-third along from base usually extending from costal margin to subcostal vein but sometimes less developed; second band half way along usually reaches from costal margin to second cubitus but may be obscure or poorly developed; apical third of tegmen clear or speckled. Hind wing fascia (Fig. 6) incomplete, interrupted between first cubitus and first anal vein (in *O. plenus browni* more broadly interrupted or almost obsolete), reaching hind margin of wing posteriorly; basal area pale yellow or colourless, wing tip sometimes infumate. Hind femur with irregular transverse oblique bands on exterior surface and interior upper marginal area; interior medial area straw-coloured; ventral surface orange-red; hind tibia with dark basal ring, subbasal pale area, otherwise orange-red.

♀. Ventral ovipositor valves (Fig. 45) elongate, weakly sclerotized, longer than wide, exterior lateral margins only slightly excavated; basivalvular sclerite smooth. Spermatheca (Fig. 99) with conical, slightly recurved subapical diverticulum.

AFFINITIES. *O. plenus* is a member of the rather homogeneous group of species which includes *O. senegalensis* and *O. nigeriensis,* but is in some respects intermediate between this group and the *O. instillatus-obtusangulus-rosescens*-group, having a tendency to overall grey-brown coloration, with green forms rare, and epiphallic lophi with small, equal-sized lobes (Fig. 98).

DISTRIBUTION (Fig. 153, and Biogeography section, p. 156). Widely distributed in southern Africa, with a population in Tanzania, isolated on the northern edge of the *Brachystegia* woodland. The records from Namibia, Angola, and Zambia appear to be new. Johnsen & Forchhammer (1978) have recently recorded the species (as *O. dilutus*) from Botswana. The record by Dirsh (1956*a*: 325, 265) from Lesotho should be referred to *O. plenus browni* which is apparently restricted to high ground above about 1500 m in the eastern half of South Africa, and Lesotho.

BIOLOGY. Unknown. Cuthbertson (1934) reported this species among the prey of the asilid fly *Alcimus rubiginosus*.



Figs 96–99 *O. plenus*, genitalia. 96, endophallus and cingulum, lateral view; 97, same, dorsal view; 98, epiphallus; 99, spermatheca.

The two subspecies of *O. plenus* may be separated by the following key.

1 Hind wing fascia absent or restricted to posterior half of wing, seldom passing third anal vein anteriorly but occasionally reaching posterior branch of second anal vein (*2Aa*) (E. Transvaal, E. Cape Province, Lesotho) . . . . ***O. plenus browni*** subsp. n. (p. 121)

– Hind wing fascia only interrupted between first cubitus and first anal vein, reaching costal margin of wing anteriorly (southern Africa, NE. Tanzania) . . ***O. plenus plenus*** (Walker) (p. 119)

Oedaleus plenus plenus (Walker, 1870)

Epacromia plena Walker, 1870: 769. Lectotype ♂, SOUTH AFRICA (BMNH), designated by Uvarov (1925: 276) [examined].

Oedaleus (*Oedaleus*) *nigro-fasciatus* var. *caffer* Saussure, 1888: 41. LECTOTYPE ♀, SOUTH AFRICA (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1925: 276.]

Oedalus [sic] *plena* (Walker) Distant, 1892: 260.

Chortoicetes plena (Walker) Kirby, 1920*b*: 70.

Oedaleus plenus (Walker) Kirby, 1910: 225.

Oedaleus caffer Saussure; Kirby, 1910: 225.

Oedaleus dilutus Miller, 1929: 74. Holotype ♂, TANZANIA (BMNH) [examined]. **Syn. n.**

MEASUREMENTS
Sample from SW. Africa: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26·18	3·6	4·73	19·59	12·32	3·33	3·70	4·15
Range	24·3–27·4	3·3–3·8	4·3–5·1	18·3–20·7	11·2–12·85	3·1–3·6	3·5–3·9	3·8–4·6
S.D.	0·867	0·113	0·228	0·727	0·503	0·129	0·119	0·214
n	14	14	14	14	14	14	14	14

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31·44	4·72	5·76	23·48	14·6	3·9	3·75	4·08
Range	29·0–33·0	4·3–5·0	5·3–6·1	21·8–25·0	13·3–15·7	3·5–4·3	3·4–4·0	3·8–4·4
S.D.	1·202	0·188	0·239	0·887	0·676	0·234	0·194	0·177
n	15	15	15	15	15	15	15	15

MATERIAL EXAMINED

Epacromia plena Walker, lectotype ♂, **South Africa:** no further data (*Smith?*) (BMNH). *Oedaleus nigrofasciatus* var. *caffer* Saussure, lectotype ♀, **South Africa:** no further data (*Delalande*) (MHN, Geneva). *Oedaleus dilutus* Miller, holotype ♂, **Tanzania:** Dodoma, Kitope, 6.iv.1927 (*Miller*) (BMNH).

In addition to the types, 276 specimens were examined from the following localities. **South Africa:** 3 ♂, 2 ♀, no further data (*Smith?*) (including 2 ♂, 2 ♀, paralectotypes of *Epacromia plena* Walker); 1 ♂, 'Cape', no further data (paralectotype of *E. plena* Walker); Transvaal, Rustenburg; T., Wyllies Poort; T., Pretoria; T., Tom Burke, 23°04′S, 28°00′E; T., Johannesburg; T., Klaserie, nature area, Klaserie R.; T., 24·2 km W. of Pongola, 550 m; T., 33·8 km S. of Messina, 660 m; T., 3·2 km S. of Messina, 590 m; T., 17·7 km N. of Louis Trichardt, 800 m; T., Skukuza; T., Zebediela; T., Messina; T., Metsimaklaba; Cape Province, Ceres; C.P., Nieuwoudtville; C.P., Queenstown, 1050 m; C.P., 8 km NW. of Craddock; C.P., Grahamstown; C.P., 35·4 km W. of Cofimvaba, 940 m; C.P., Cape of Good Hope; C.P., Namaqualand; C.P., Spektakel Pass, 29 km W. of Springbok; C.P., Skeerpoort. **Namibia:** Gobiswater farm, 19·3 km N. of Grootfontein; Kombat; 17°59′S, 16°02′E, 1110 m; Swakop R., 4·8 km S. of Okahandja; Rietfontein, 37 km SW. of Grootfontein; Otavie; Okahandja; Damaraland, c. 8 km W. of Grootfontein, 1470 m; Otjitambi farm, 43·5 km ESE. of Kamanjab; Otjikoko Süd farm, 53 km ENE. of Omaruru; Regenstein, 24 km SSW. of Windhoek; Onguma farm, 88·6 km NW. of Tsumeb; Ameib farm; 30·6 km NW. of Karibib; 25·8 km E. of Gobabis; 3·2 km NW. of Ontjo, 1250 m; 9·7 km W. of Windhoek, 8.v.1958, 1660 m; 60 km W. of Windhoek, 14.iii.1972; 13 km N. of Rehoboth; 50 km W. of Omaruru; Okahandja bis, Waterberg; Namib. **Botswana:** Maun; Gaberones; Nokaning; Selinda spillway; Kwebe Hills; Kasana; Ngamiland, 20°S, 23°E; Ghanzi, Mongalatsiba; Kalahari; 59·6 km S. of Francistown, 21°37′S, 27°21′E; L. Ngami, 19·3 km NE. of Sehithwa; 29 km NE. of Kalkfontein; 16 km NE. of Ghanzi; Moremi reserve, 19°23′S, 23°33′E; 40·3 km W. of Gweta, 20°17′S, 25°54′E: Kuke pan, 20°59′S, 22°25′E; 67·6 km W. of Kalkfontein; 4·8 km NE. of Maun; nr Moremi res., 19°27′S, 23°45′E; Kaotwe. **Angola:** Tundavala, 13–16 km NW. of Sa da Bandeira; Rocadas, mopane scrub; Otchifengo R., Iona Nat. Pk; Huila distr., Cahama. **Zimbabwe:** Odzi distr., Matopo Hills; Shamva, 930 m; Victoria Falls, 900 m; Shangani, de Beers ranch; Selukwe, 1120 m; Balla Balla; 22·5 km NW. of Beitbridge, 540 m; 87 km S. of Umtali, 560 m; West Nicholson, Masase. **Zambia:** Livingstone. **Tanzania:** 1 ♀, Tindiga, 20.xi.1926 (*Miller*) (paratype of *O. dilutus* Miller); S. of Usasi, clearings, 72·5 km NW. of Singida; Kondoa to Irangi; Ruaha Nat. Pk.

DISCUSSION. Walker's type-material almost certainly came from south-west Cape Province. Specimens from this climatically distinct zone usually have the posterior arms of the pronotal X-marking thin, less than one and a half times as wide as the anterior arms, whereas elsewhere the posterior arms are usually about three times as wide as the anterior arms. Despite the evident discontinuity in the distribution of this character (Fig. 153) it is not an absolutely reliable distinction between populations, so the name *O. plenus plenus* is here used to refer to all the material available whatever its pronotal characteristics, except for material referred to *O. plenus browni* for other reasons.

Miller's *O. dilutus,* described from Tanzania, is identical in all respects with material from south of the *Brachystegia* woodland zone and is here considered to be a junior synonym of *O. plenus plenus.* If the SW. Cape population should later be conclusively shown to have consistent characters meriting subspecies status then the name *O. plenus plenus* could be restricted to this population and *dilutus* would again be available for material of the species from other areas. Measurements of eight males and seven females from SW. Cape Province, including Walker's type-series, were found to give rather high mean values for the length/depth ratio of the hind femur (FL/FD: 4·00 ♂, 4·09 ♀). There is, however, a likelihood of bias with such low numbers and dubious locality data and a study of fresh material from this area is needed.

O. nigrofasciatus var. *caffer* Saussure, 1888, synonymized with *O. plenus* by Uvarov (1925), was originally described from 'Africa meridionalis'. There are several specimens of *O. plenus* in the MHN, Geneva, of which only one female is labelled in Saussure's own hand '*var. afr. merid.*'. This specimen is accordingly here designated as the lectotype of *O. nigrofasciatus* var. *caffer.* The status of the remaining material (3 ♂, 7 ♀) in the MHN Geneva is not clear and paralectotypes have therefore not been designated.

Oedaleus plenus browni subsp. n.

MEASUREMENTS (type-series)

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·16	3·74	4·57	16·85	12·26	3·51	3·49	3·73
Range	22·2–24·1	3·3–4·1	4·2–5·1	15·8–18·1	11·1–13·6	3·3–3·9	3·3–3·6	3·5–4·0
S.D.	0·658	0·247	0·287	0·769	0·742	0·188	0·111	0·168
n	6	9	9	7	9	9	9	7

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	30·28	5·22	5·81	21·92	15·13	4·27	3·55	3·78
Range	29·1–31·6	4·8–5·6	5·1–6·3	20·3–24·0	14·0–15·9	3·9–4·6	3·4–3·7	3·5–4·0
S.D.	1·012	0·275	0·461	1·489	0·703	0·246	0·116	0·164
n	5	6	6	6	5	5	5	6

MATERIAL EXAMINED.

Holotype ♂, **South Africa:** Cape Province, De Aar, 13.ii.1959 (*Brown*) (DATS, Pretoria).

Paratypes, **South Africa:** 3 ♂, 1 ♀, Orange Free State, Bosrand, Afdeling farm, 30.iii.1934 (*Ogilvie*); 1 ♂, O.F.S., Mafeking, 28.ii.1934 (*Ogilvie*); 1 ♂, O.F.S., Bloemfontein, 13.ii.1918; 1 ♀, same data, 10.iv.1918; 1 ♂, same data, 13.iv.1951 (*Botha*); 1 ♀, O.F.S., Petrus, 23.i.1919; 1 ♂, O.F.S., Bloemfontein, xii.1931 (*Key*) (ANIC, Canberra); 1 ♀, Transvaal, Pretoria (*Distant*); 1 ♀, Cape Province, De Aar, 13.ii.1959 (*Brown*) (DATS, Pretoria); 2 ♂, C.P., 22·5 km E. of Middleburg, 8–14.xii.1960 (*Brown, Fürst & Haacke*) (DATS, Pretoria). **Lesotho:** 1 ♀, Maseru, Lancer's Gap, 22.iii.1951 (*Brinck & Rudebeck*).

DISCUSSION. In addition to the characters mentioned in the key, interesting differences between the morphometrics of *O. plenus browni* and the nominate subspecies are revealed when mean measurements are compared by 't' test. Femur length and pronotum length do not differ significantly, but in females head width is very significantly greater in *O. p. browni* than in *O. p. plenus* ($P < 0{\cdot}001$), while tegmen length is significantly less, particularly in the male ($P < 0{\cdot}001$ ♂, $< 0{\cdot}05$ ♀). Head width variation is enigmatic, but decrease in wing length is very commonly associated with adaptation to montane conditions in grasshoppers at and below species level. Not surprisingly TL/PL is significantly greater in the nominate subspecies ($P < 0{\cdot}001$ ♂, $< 0{\cdot}002$ ♀) than in *O. p. browni* but less accountably the FL/FD ratio is also higher in the former than the latter

($P<0{\cdot}001$ ♂, $<0{\cdot}002$ ♀). Presumably decreasing flight capability is correlated with decreased take-off capability in the form of shorter femora.

The new subspecies is named in honour of its discoverer, Dr H. D. Brown.

Oedaleus decorus (Germar, 1826)
(Figs 11, 28, 29, 51, 100–106, 158, 163)

Acrydium decorum Germar, 1826: pl. 17.

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two-fifths of maximum width anteriorly; lateral carinae distinct, faint median carina sometimes visible; frons in profile straight or slightly convex; frontal ridge, slightly expanded and coarsely punctate between antennal bases. Eyes about one and two-fifths as long as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus. Tegmen surpassing hind knees by about one-third of femur length. Hind tibia with 11–12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment about twice claw length; arolium half claw length. Cerci about twice as long as basal width. Genitalia (Figs 100–105): cingular apodemes normal, rami well developed, cingular and apical penis valves short; subapical ventral process small; epiphallus variable, trapezoidal, with thick bridge; inner and outer lobes of lophi of equal size; anterior projections large, rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on frons, genae, pronotum, basal quarter of tegmina, and hind femora. Tegmen infuscate brown in basal half with variable transverse pale bands situated one-sixth, one-third, and one-half along from base; apical half clear with brown specks. Hind wing fascia (Fig. 11) complete, not reaching hind margin of wing, wing tip tinged with brown; basal area of wing pale yellow with distinct pale bluish tinge on wing vein bases. Hind femora with three oblique transverse bands on inner and outer surfaces, ventral surface red, knees black; hind tibiae with black basal ring, basal one-third pale straw-coloured, apical two-thirds reddish.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 51) blunt, strongly sclerotized. Spermatheca (Fig. 106) with apical diverticulum bulbous with acutely rounded apex, and short subapical diverticulum.

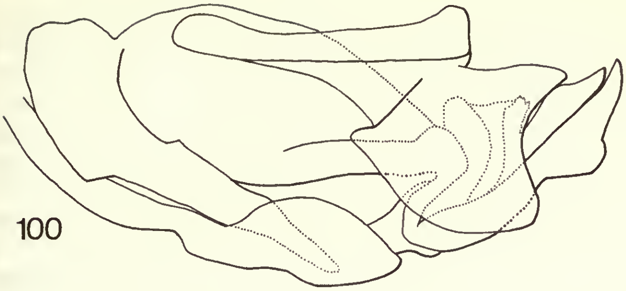
AFFINITIES. *O. decorus* is most closely allied to *O. senegalensis, O. nigeriensis* and *O. infernalis* in having strongly transverse inner lobes to the epiphallic lophi. The red ventral surface of the hind femur is shared with *O. infernalis* from which, however, *O. decorus* is easily distinguished by its general coloration, and the form of the pronotal X-marking and hind wing fascia.

DISTRIBUTION (Figs 158, 163, and Biogeography section, pp. 161, 165). Europe, North Africa, Middle East, with subspecies *decorus* extending into SW. Russia, and subspecies *asiaticus* continuing eastwards across Transbaikalia, Mongolia and China.

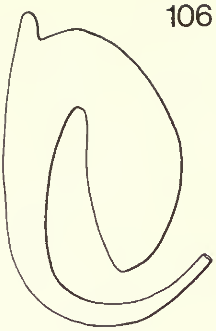
BIOLOGY. *O. decorus* has probably received more attention than any other species in the genus except *O. senegalensis.* Adults of *O. decorus decorus* are found in North Africa from June until January and in the Middle East from April to September. In southern Europe they occur from May to October with a gradually shortening and later season towards the northern limit of the species. *O. decorus asiaticus* has been recorded in eastern U.S.S.R., Mongolia, and China from July to September. It is probable that one generation is the norm outside Africa. However, the longer season in North Africa may allow a second generation, since laying has been reported in July (A-L.R.C. Unpublished Report 6114-135) in Libya. Berezhkov (1956) gives five as the number of nymphal instars. The egg pod has been described by Zimin (1938), and Morales Agacino (1951), who found 10 to 35 eggs per pod. Waloff (1954) records 18 and 20 ovarioles per ovary in two females dissected.

Ivanov (1934) made a study of the biology and ecology of *O. decorus* in Central Asia and Stebaev (1957) found that it was seasonally mobile between different types of habitat. It was recorded in the

Figs 100–106 *O. decorus,* genitalia. 100–102, *O. decorus decorus*; (100) endophallus and cingulum, lateral view; (101) same, dorsal view; (102) epiphallus. 103–105, *O. decorus asiaticus*; (103) endophallus and cingulum, lateral view; (104) same, dorsal view; (105) epiphallus. 106, *O. decorus decorus,* spermatheca.

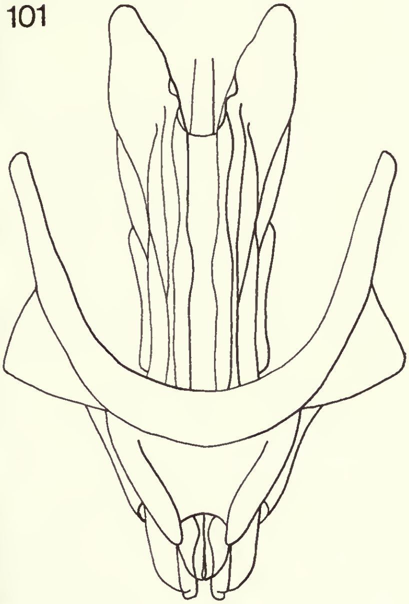


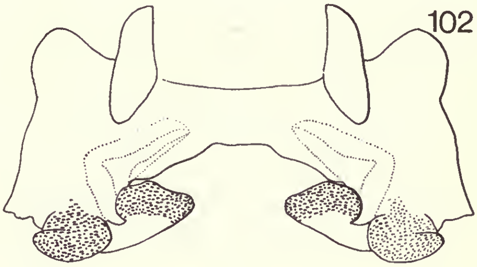
100



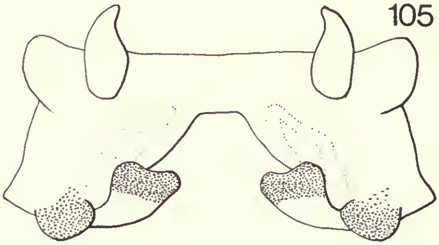
106

101



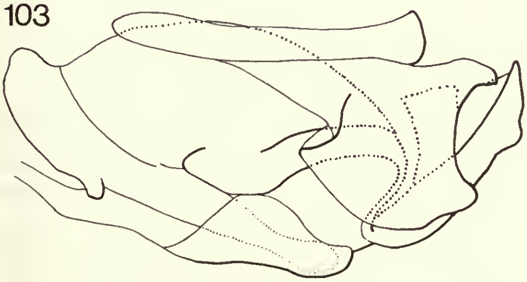


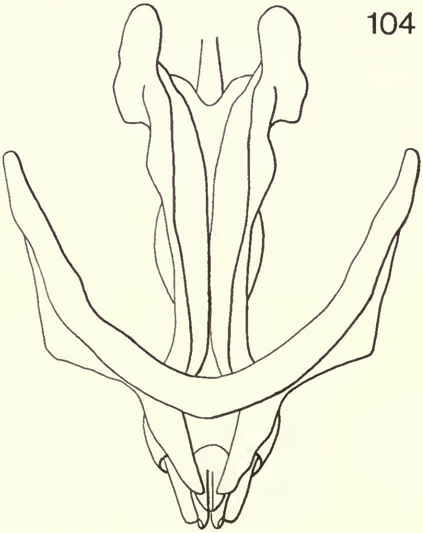
102



105

103





104

French Alps up to 1300 m by Dreux (1961) who stated that the species distribution in France is bounded by the 16° July isotherm. In U.S.S.R. Bei-Bienko & Mishchenko (1951*a*) regarded it as a characteristic species of stony mountain sides with xerophytic vegetation, and in the Pyrenees Marty (1969) found that this species constituted 20% of all Orthoptera in the littoral zone. In Turkestan (Zacher, 1949) the species lays in damp areas with *Cynodon dactylon* and *Hordeum murinum. O. decorus* has been reported damaging wheat, vines and lentils in Libya (A-L.R.C. Unpublished Report 6114-135), maize and tobacco in Morocco (Lépiney & Mimeur, 1932) and cotton, lucerne and wheat in Iran (Farahbaksh, 1961). *O. decorus asiaticus* was described as a pasture pest in Transbaikal region (Bei-Bienko & Mishchenko, 1951*b*). Predation of adults of *O. decorus* by asilid flies was reported by Adamovic (1968) and four species of *Blaesoxipha* (Greathead, 1963; Léonide & Léonide, 1969; 1973) and one Nemestrinid (Léonide, 1963) have been reared from adults. Integumental coloration in relation to humidity, temperature, and background colour have been studied by Jovančić (1953) and Ergene (1954; 1955*a*; 1955*b*; 1955*c*; 1956). The thoracic repugnatorial gland has been described by Vosseler (1902*c*), and Hollande (1926) who mistakenly considered the gland to be eversible.

The two subspecies of *O. decorus* may be separated by the following key.

1 Generally larger (except in northern France), body length 24·0–36·3 mm male, 31·1–49·0 mm female; pronotal hind margin more angular (Fig. 28); hind wing fascia thicker, and terminating posteriorly within 1 mm of wing margin (Fig. 11); interior surface of epiphallic bridge weakly arched (Fig. 102) (North Africa, S. Europe, Middle East, SW. U.S.S.R. as far as E. Kazakh S.S.R., W. Sinkiang province of China). . . . . **O. decorus decorus** (Germar) (p. 124)

– Generally smaller, body length 25·0–27·5 mm male, 32·0–37·6 mm female; pronotal hind margin more rounded (Fig. 29); hind wing fascia thinner, terminating posteriorly more than 1 mm from wing margin; interior surface of epiphallic bridge strongly arched (Fig. 105) (Mongolia, Transbaikalia, Hopeh and Shantung provinces of China). . **O. decorus asiaticus** Bei-Bienko (p. 126)

Oedaleus decorus decorus (Germar, 1826)

Acrydium decorum Germar, 1826: pl. 17. Holotype ♂ (?), U.S.S.R.: 'Podolia australi (*Besser*)' '(Mus. Besseri)' (lost). NEOTYPE ♂, U.S.S.R.: Daghestan (BMNH), here designated [examined].

[*Acridium flavum* (Linnaeus); Costa, 1836: 11. Misidentification.]

[*Oedaleus nigrofasciatus* (Degeer); Bormans, 1879: 407; Brunner, 1882: 169; Bonnet & Finot, 1884: 220; Bormans, 1884: 179; 1885: 109; Olivier, 1892: 45; Frey-Gessner, 1894: 106; Finot, 1895: 479; Krauss & Vosseler, 1896: 531; Fenard, 1896: 107; Bolívar, 1898: 76; Burr, 1898: 179; Vosseler, 1902*a*: 359; 1902*b*: 116; 1902*c*: 84; Finot, 1902: 434; Giglio-Tos, 1907: 8; Burr, 1912: 31; Bolívar, 1914: 188; Werner, 1914: 397; Steck, 1915: xiv; Plotnikov, 1921: 9; Giglio-Tos, 1923: 5; Rabaud, 1923: 18; Zanon, 1924: 246; Salfi, 1925: 93; Hollande, 1926: 374; Werner, 1934: 6; Jovančić, 1953: 99; Barbut, 1954: 339; Costantino, 1954: 4. Misidentifications.]

[*Oedipoda nigrofasciata* (Degeer); Serville, 1831: 288; Burmeister, 1838: 645. Misidentifications.]

[*Acrydium nigrofasciatum* (Degeer); Latreille, 1805: 157. Misidentification.]

[*Gryllus nigrofasciatus* (Degeer); Charpentier, 1825: 140. Misidentification.]

[*Gryllus flavus* (Linnaeus); Rambur, 1838: 82. Misidentification; Uvarov, 1948: 384.]

Oedaleus decorus (Germar) Uvarov, 1923: 69.

MEASUREMENTS

Sample from Algeria: Djelfa, 9.x.38 (*M. N. Korsakoff*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38·2	5·69	6·23	28·27	18·86	4·42	4·27	4·56
Range	32·8–	5·1–	5·2–	23·6–	16·3–	3·8–	4·0–	4·1–
	43·2	6·2	7·4	31·3	21·7	5·1	4·6	5·0
S.D.	2·55	0·27	0·525	1·890	1·39	0·32	0·17	0·17
n	27	27	27	23	26	26	26	23

Females

Mean	44·25	7·09	7·26	31·93	21·47	5·16	4·16	4·47
Range	40·8–	6·4–	6·4–	30·0–	19·0–	4·7–	3·8–	4·3–
	48·8	8·0	8·5	35·9	24·9	5·8	4·5	4·8
S.D.	2·66	0·38	0·61	1·86	1·64	0·34	0·18	0·14
n	24	28	28	14	28	28	28	14

Sample from France: Gironde, S. of Soulac-sur-Mer, 11.viii.77 (*N. D. Jago*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·0	3·81	4·25	18·58	12·65	3·12	4·06	4·88
Range	23·9–	3·6–	3·9–	17·8–	11·6–	2·9–	3·7–	4·6–
	26·7	4·2	4·8	20·3	14·1	3·3	4·3	5·1
S.D.	0·748	0·181	0·239	0·657	0·726	0·148	0·164	0·169
n	10	10	10	10	10	10	10	10

Females

Mean	34·17	5·33	5·82	25·28	16·75	4·20	3·99	4·74
Range	32·7–	5·1–	5·3–	24·3–	16·0–	3·9–	3·8–	4·6–
	35·6	5·5	6·2	26·5	17·4	4·5	4·3	4·9
S.D.	1·070	0·115	0·272	0·823	0·412	0·164	0·129	0·096
n	12	13	13	12	13	13	13	12

Sample from France: Bouches-du-Rhône, 22 km SE. of Arles, 1–17.vii.60 (*B. M. Goodings & D. J. Philpot*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28·43	4·42	4·56	20·76	14·65	3·47	4·24	4·55
Range	27·0–	4·2–	4·1–	18·4–	13·3–	3·2–	4·0–	4·1–
	31·4	4·7	5·0	23·3	15·6	3·8	4·6	4·9
S.D.	1·42	0·14	0·23	1·35	0·57	0·16	0·15	0·21
n	13	13	13	13	13	13	13	13

Females

Mean	40·85	6·49	6·75	30·31	20·69	4·75	4·37	4·5
Range	38·3–	6·0–	6·1–	28·5–	19·0–	4·2–	4·0–	4·2–
	42·9	6·8	7·2	31·9	21·8	5·2	5·1	4·8
S.D.	1·54	0·25	0·48	1·13	0·92	0·34	0·36	0·18
n	8	8	8	8	8	8	8	8

Sample from Western U.S.S.R.: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27·92	4·31	4·44	20·6	14·26	3·39	4·23	4·66
Range	26·1– 30·4	3·9– 4·7	3·9– 5·1	18·9– 22·5	12·9– 15·7	3·0– 4·0	3·5– 4·5	4·2– 5·2
S.D.	1·35	0·28	0·37	1·16	0·92	0·32	0·32	0·35
n	8	8	8	8	7	7	7	8

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38·87	6·22	6·27	28·8	19·16	4·57	4·2	4·61
Range	33·0– 42·1	5·1– 6·9	4·9– 7·1	24·8– 30·9	15·7– 20·7	3·65– 5·0	4·0– 4·3	4·3– 5·1
S.D.	2·64	0·47	0·61	1·9	1·62	0·45	0·13	0·29
n	9	9	9	9	7	7	7	7

MATERIAL EXAMINED

Acrydium decorum Germar, neotype ♂, **U.S.S.R.:** Daghestan, Chodz-Tau, 5.vii.1924 (*Riabov*) (BMNH).

In addition to the neotype, a total of 750 specimens of this subspecies were examined from the following countries: **Morocco, Algeria, Tunisia, Libya, Lebanon, Syria, Israel, Iraq, Turkey, Iran, Afghanistan, U.S.S.R., Rumania, Bulgaria, Greece, Albania, Yugoslavia, Czechoslovakia, Switzerland, Italy, Sicily, Corsica, France, Spain, Portugal, Madeira, Canary Is.**

DISCUSSION. The measurements and 't' tests indicate the very considerable range of variation in morphometrics shown by this subspecies. The largest specimens, judged by femur or tegmen length, are found in Algeria, but from here northwards through western Europe there is a decline in size, with specimens from Gironde on the west coast of France significantly smaller than those from the Rhône delta in all respects, and with a significantly higher ratio of tegmen length to pronotum length and a significantly thicker femur in relation to its length. Surprisingly, the Rhône delta specimens are closest to those from the western U.S.S.R. in all measurements though differing significantly from them in the female femur length.

The type-material of *Acrydium decorum* has not been mentioned in the taxonomic literature since Germar's original description (1826) apart from repetition of the details given by him. The material was in the collection of V. S. Besser which later passed to the Zoological Museum of Kiev State University. I am indebted to Dr L. Pisareva for the information that the type cannot be found there. Since the type-material of this species is no longer extant a neotype is here designated from the south-west U.S.S.R.

Oedaleus decorus asiaticus Bei-Bienko, 1941 **stat. n.**

Oedaleus asiaticus Bei-Bienko, 1941: 152. Holotype ♂, U.S.S.R.: Buryat A.S.S.R., Kiakhta distr., Ust' Kiakhta, 20.viii.29 (*A. N. Strakhovsky*), (ZI, Leningrad).

MEASUREMENTS (all available material)

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·73	3·65	3·84	19·11	12·09	2·85	4·24	4·98
Range	24·9– 27·5	3·5– 3·8	3·6– 4·2	18·2– 21·0	11·7– 12·5	2·8– 2·9	4·1– 4·4	4·7– 5·3
S.D.	0·926	0·071	0·22	0·95	0·25	0·034	0·12	0·19
n	6	6	6	6	5	5	5	6

Females

Mean	35·79	4·41	5·57	26·33	16·29	3·75	4·34	4·74
Range	32·1–37·7	4·9–5·8	4·9–5·8	23·9–28·4	14·9–18·2	3·4–4·1	4·2–4·5	4·5–5·1
S.D.	1·80	0·26	0·37	1·24	0·92	0·19	0·082	0·175
n	9	9	9	9	9	9	9	9

Significance levels of 't' tests on comparisons of mean measurements of populations of *O. decorus*

Paired comparisons of mean values	Sex	Head width	Pronotum length	Tegmen length	Femur length	FL/FD	TL/PL
Algeria/Bouches du Rhône	♂	< 0·001	< 0·001	< 0·001	< 0·001	n.s.	n.s.
	♀	< 0·001	< 0·02	< 0·02	n.s.	n.s.	n.s.
BDR/Gironde	♂	< 0·001	< 0·01	< 0·001	< 0·001	< 0·02	< 0·001
	♀	< 0·001	< 0·001	< 0·001	< 0·001	< 0·01	< 0·01
BDR/Russia	♂	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	♀	n.s.	n.s.	n.s.	< 0·05	n.s.	n.s.
Gironde/Russia	♂	< 0·001	n.s.	< 0·001	< 0·002	n.s.	n.s.
	♀	< 0·001	n.s.	< 0·001	< 0·002	< 0·01	< 0·05
Gironde/*asiaticus*	♂	< 0·05	< 0·01	n.s.	< 0·05	< 0·05	n.s.
	♀	n.s.	n.s.	< 0·05	n.s.	< 0·001	n.s.
Russia/*asiaticus*	♂	< 0·001	< 0·01	< 0·05	< 0·001	n.s.	< 0·05
	♀	< 0·001	< 0·01	< 0·01	< 0·001	< 0·05	n.s.

MATERIAL EXAMINED

U.S.S.R.: 1 ♀, Transbaikal reg., mouth of R. Kïran, 10.ix.1929 (*Mikhno*) ZI, Leningrad) (paratype of *Oedaleus asiaticus* Bei-Bienko); 1 ♂, 1 ♀, Transbaikal reg., Ust' Kyakhta dist., 20.vii.1929 (*Strakhovskiy*) (ZI, Leningrad) (paratypes of *O. asiaticus* Bei-Bienko); 1 ♀, Transbaikal reg., Troitskosavsk dist., 28.viii.1929 (*Mikhno*); 1 ♂, Minusinsk steppe, 29.vii.1924 (*Filipyev*); 1 ♂, Minusinsk, 30.vii.1924 (*Filipyev*) (ANS, Philadelphia); 1 ♀, same data, 21.viii.1924 (ANS, Philadelphia); 2 ♀, Transbaikal reg., Ust' Kyakhta dist., 20.viii.1929 (*Strakhovskiy*) (ANS, Philadelphia); 1 ♀, Troitskosavsk dist., Kapcheranka, 4.ix.1929 (*Mikhno*) (ANS, Philadelphia); 1 ♂, Minusinsk, Tagarsk I., 21.viii.1924 (*Filipyev*). **Mongolia:** 1 ♂, 1 ♀, Altai reg., W. foothills of Ikhe Bogdo, 21.viii.1926 (*Kiprichenko*) (ZI, Leningrad) (paratypes of *O. asiaticus* Bei-Bienko). **China:** 1 ♂, Peiping, 2.viii.1934 (*Chang?*) (USNM, Washington); 1 ♀, Shantung pr., O-ku, 18.viii.1934 (*Chang?*) (USNM, Washington).

DISCUSSION. Material of *O. decorus asiaticus* from eastern U.S.S.R. and China differs significantly in all measurements from material of the nominate subspecies in the western U.S.S.R., although in the two ratios differences are less marked. This might suggest morphometric support for the separate species status of *asiaticus*, but overall there is an equally significant difference between the western U.S.S.R. material and that from the Gironde region of western France. Comparing material of *asiaticus* with Gironde specimens, differences are generally of low significance (< 5 > 2%) or none at all excepting pronotum length, which in male *asiaticus* is markedly smaller, and the femur length to depth ratio (FL/FD), which is significantly smaller in the Gironde population than in *asiaticus*.

Bei-Bienko & Mishchenko (1951*b*: 578, 579) distinguish *asiaticus* from *decorus* on the basis of minor differences of coloration and shape which have not been found reliable in the material used in this study. At present *asiaticus* is considered as a subspecies or race of *decorus* but may prove on further study not to justify even racial status. Its small size and rounded posterior angle of the pronotum are features also found in specimens from Gironde and elsewhere on the north-western limit of the species distribution in France, and are probably a response to harsh conditions in both cases.

Oedaleus infernalis Saussure, 1884
(Figs 5, 36, 52, 107–110, 163)

Oedaleus (*Oedaleus*) *infernalis* Saussure, 1884: 116. LECTOTYPE ♂, JAPAN (NM, Vienna), here designated [examined].

Oedaleus (*Oedaleus*) *infernalis* var? Saussure, 1884: 117. [Based on 1 ♂, U.S.S.R.: Amur (NM, Vienna), see below.]

Oedaleus infernalis var. *amurensis* Ikonnikov, 1911: 255. LECTOTYPE ♂, U.S.S.R.: Amur (NM, Vienna), here designated [examined]. [Varietal name erroneously attributed to Saussure, op. cit.] **Syn. n.**

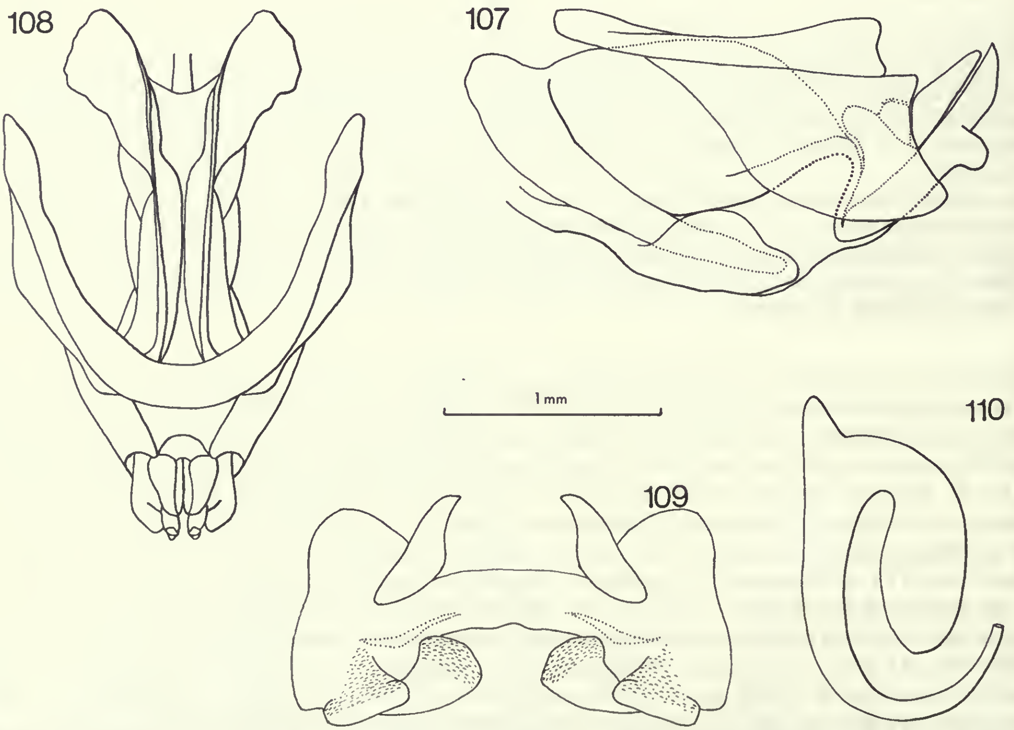
Oedaleus infernalis amurensis Ikonnikov; Bei-Bienko, 1941: 154.

Oedaleus manjius Chang, 1939: 21. Holotype ♂, CHINA: Chekiang, Wenchow, 15.ix.1933 (*K. S. Chang*) (lost). **Syn. n.**

Oedaleus infernalis montanus Bei-Bienko *in* Bei-Bienko & Mishchenko, 1951*b*: 577. Holotype ♂, CHINA: N. slope of Burkhan-Budda, defile Khatu, *c.* 10,800 ft [3300 m], end vi- beginning vii. 1901 (*P. C. Kozlov*) (ZI, Leningrad). **Syn. n.**

Oedaleus infernalis Saussure; Jacobson & Bianchi, 1905: 256.

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together; flagellum 24-segmented. Fastigium of vertex as long as wide, concave with raised margins, narrowing to half maximum width anteriorly. Frons in profile convex, frontal ridge constricted at vertex and below median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, lateral lobes coarsely punctate in metazona, hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one-quarter to one-half of hind femur length. Hind tibia with 12 inner and 12 outer spines; inner apical spurs less than twice length of outer; apical tarsal segment more than two and a half times claw length; arolium little more than half claw length. Cerci about twice as long as wide. Genitalia (Figs 107–109): rami, apodemes, cingular and apical penis valves of moderate length; subapical process large and protruding; epiphallus rectangular, twice as long as wide; outer lobes of lophi wider than inner lobes; anterior projections large, rounded; posterior projections small.



Figs 107–110 *O. infernalis*, genitalia. 107, endophallus and cingulum, lateral view; 108, same, dorsal view; 109, epiphallus; 110, spermatheca.

General coloration dark mottled brown, occasionally green. Brown form with pale X-marking on pronotum (♀, Fig. 36), and pale band on genae; green form with variable degree of green on frons, genae, pronotum (obscuring X-marking), thorax and hind femora. Tegmen infuscate in basal half with four variable pale transverse bands extending from costal margin. First band one-sixth along from base, reaching subcostal vein, sometimes obsolescent; second band one-third along, reaching first or second cubitus; third band half along, reaching *Cu1c* or *Cu2*; fourth band two-thirds along, variable, often reaching hind margin but without a distinct border towards apex of wing which is clear with variable dark patches. Hind wing fascia (Fig. 5) complete; wing tip infumate, basal area pale yellow. Hind femur with 3 variable oblique transverse dark bands on external and internal surface. On internal surface two basal bands combine to form U-shaped marking in medial area. Ventral surface of hind femur red, sometimes faded; hind knees black; tibiae basally black, subbasally pale straw (sometimes tinged with red), remainder red.

♀. Hind tibiae and ventral surface of hind femur brown, not red. Ventral ovipositor valves (Fig. 52) elongated and ridged; basivalvular sclerite rugose. Spermatheca (Fig. 110) with short conical subapical diverticulum.

MEASUREMENTS

Sample from Japan: Nishigo, Uzen.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31·45	4·43	5·73	23·37	16·52	4·18	3·95	4·08
Range	28·7–	4·2–	5·3–	21·2–	15·2–	3·9–	3·8–	3·8–
	34·8	4·7	6·2	26·3	17·8	4·5	4·2	4·4
S.D.	1·377	0·144	0·259	1·229	0·697	0·155	0·109	0·142
n	21	21	21	21	21	21	21	21

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	42·29	6·28	7·88	31·28	22·03	5·37	4·10	3·97
Range	38·6–	6·0–	7·4–	28·0–	20·7–	5·0–	3·9–	3·7–
	45·8	6·9	8·7	34·1	25·5	6·0	4·3	4·2
S.D.	1·912	0·246	0·378	1·616	1·146	0·242	0·113	0·157
n	19	19	19	19	19	19	19	19

Sample of '*amurensis*', from E. Manchuria and Ussuri region of U.S.S.R. around L. Khanka, including lectotype.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·9	3·71	4·66	19·01	12·98	3·30	3·96	4·08
Range	23·7–	3·5–	4·2–	17·1–	11·9–	3·0–	3·5–	3·4–
	30·6	4·1	5·1	23·2	14·3	3·65	4·3	4·4
S.D.	1·957	0·163	0·350	1·608	0·870	0·178	0·185	0·158
n	12	13	13	13	13	12	12	13

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38·71	5·66	7·05	28·65	18·58	4·71	3·95	4·06
Range	34·5–	5·2–	6·3–	25·3–	17·2–	4·3–	3·6–	3·8–
	46·8	6·4	8·2	35·7	19·1	5·3	4·2	4·4
S.D.	3·806	0·394	0·654	3·295	1·180	0·319	0·163	0·201
n	10	10	10	10	9	9	9	10

Sample of '*montanus*' ♂ paratype and 2 ♀ from China: Lifan, Szechuan.

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	22·6	3·6	4·2	15·9	12·2	3·4	3·7	3·7
♀	38·3	6·2	8·0	28·1	20·6	5·6	3·7	3·5
♀	53·9	7·6	10·2	40·2	23·2	6·0	3·9	4·0

Sample of '*manjius*' from China: Szechuan, Wei Chow, 65 mls NW. of Chengtu, 5000 ft [1500 m]; viii.33 (*D. C. Graham*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26·01	4·04	5·02	18·65	13·98	3·77	3·70	3·71
Range	23·3– 29·2	3·7– 4·4	4·5– 5·8	16·5– 21·9	13·3– 14·8	3·6– 4·0	3·6– 3·8	3·4– 3·9
S.D.	2·039	0·198	0·352	1·766	0·449	0·096	0·077	0·149
n	12	12	12	12	8	8	8	12

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	36·01	5·96	7·33	25·83	18·75	5·0	3·76	3·53
Range	32·1– 40·3	5·4– 6·8	6·4– 8·4	23·3– 29·3	17·0– 20·4	4·5– 5·8	3·5– 4·2	3·3– 3·8
S.D.	2·097	0·320	0·509	1·491	1·011	0·294	0·140	0·135
n	25	25	25	25	25	25	25	25

AFFINITIES. ***O. infernalis*** is most closely related to ***O. decorus*** by its overall shape, the continuous band of the hind wing and the red ventral surface of the hind femur. It is, however, easily distinguished by its more sombre pattern, the poorly defined pronotal X-marking (Fig. 36) and hind wing fascia (Fig. 5), and the rather short cingular rami of the male genitalia (Fig. 108). The bases of the main veins of the hind wing are never tinged with pale blue in this species. In the female the ventral ovipositor valves are longer and more ridged than those of ***O. decorus*** (Figs 52, 51).

MATERIAL EXAMINED

Oedaleus infernalis Saussure, lecotype ♂, **Japan:** no further data (NM, Vienna). *Oedaleus infernalis* var. *amurensis* Ikonnikov, lectotype ♂, **U.S.S.R.:** Amur (NM, Vienna).

In addition to the types, 447 specimens were examined from the following localities. **Japan:** Tokyo; Takayama, Myjagi; Nagasaki; Yamashiro I., Kyoto; Yokohama; Nishigo, Uzen; Yamanaka Lake, Honshiu; 2 ♀, 'Japan', no further data (NM, Vienna) (paralectotypes of *Oedaleus infernalis* Saussure). **U.S.S.R.:** Kamen-Rybolov, L. Khanka, S. mouth; Ussuri Region, Spassk distr., Yakovlevka, woodland in inundation zone of R. Daubikhe; E. Siberia, Ussuri Reg., Spassk distr., Schmakovka; Ussuri Reg., R. Lyan-chi-khe; Siberia, 44°30′N, 133°00′E; E. Siberia, Kamen-Rybolov. **China:** Shense Pr., Taipaishan; N. Chihli Pr., Chih Feng; Chee Foo; Manchuria, Kuangning; Manchuria, L. Khanka; Nanking; Tientsin; Peking; 14 ♂, 50 ♀, 5 nymphs, Szechuan, Wei-Chow, 105 km N. of Chengtu, 1500 m, viii.33 (*Graham*) (USNM, Washington) (1 ♀ labelled '*Oedaleus wenchowensis* Chang det. Chang 1936'); Szechuan, Wenchuan; Szechuan, Wen Chuan Shien, 48 km NNW. of Kuan Shien, 1500–2250 m; Szechuan, Wei Chow, 105 km NW. of Chengtu, 1650–2700 m; Szechuan, between Li Fan and Wen Chuan Shien, 48·3 km NNW. of Kuan Shien, 1650–1950 m; Szechuan, O-Er, 42 km N. of Li Fan, 2700 m; Szechuan, Suifu; Peiping, Yenching University; Chekiang, Unchia; Chekiang, Ching'tien; Shantung; Mt Foochow; Mice River flats, Fu-chou, Fukien; Szechuan, Mt Omei, Baian-kara-ula range; Szechuan, Kwanhsien, 900m; Szechuan, nr Wenchuan, 1500–2100 m; Tseo Jia Geo, S. of Suifu, 420–600 m; Kong Shien, S. of Suifu, 420 m; 1 ♂, Szechuan, Li Fan, 10.viii.1893 (*Potan*) (ZI, Leningrad) (paratype of *Oedaleus infernalis montanus* Bei-Bienko); Ming tomb; Manchuria, Chin San; Foochow; Shantung peninsula, Yen-t'ai (Chefoo); Kiautschougebiet, Tsingtau; E.

China, Chen-Kia-tchouanc. **Mongolia:** no further data. **Korea (South):** Port Lazareff, 19·3 km from Gensan; Palgong San, 13 airline km N. of Taegu, 1200 m; Palgong San, 16 airline km N. of Taegu, 750 m.

DISTRIBUTION (Fig. 163, and Biogeography section, p. 163). Widely distributed in SE. Asia.

BIOLOGY. Little is known of the biology of this species. Adults are found from July to October. There are records of damage to citrus (Chen & Wong, 1936), rice (Cheo, 1937; Shiraki, 1952) and sugar cane (Butani, 1961; Box, 1953), the last from almost every country in which the insect is found. The records of rice damage in Taiwan (Box, 1953; Bei-Bienko & Mishchenko, 1951*a*; Cheo, 1937) have not been confirmed by examination of specimens during this study, though the species may be expected to occur there. Genetical studies of *O. infernalis* have been made by Lu (1951–2), Kawamura (1957), Takizawa & Narasawa (1971), and Inoue (1972). The Meloid beetle *Epicauta gorhami* was recorded as an egg predator in Japan (Nagatomi & Iwata, 1958).

DISCUSSION. At the commencement of this study there were two recognized subspecies of *O. infernalis*, and one closely related species, *O. manjius* Chang. All three taxa are here synonymized because the characters given by Chang (1939) and by Bei-Bienko & Mishchenko (1951*b*) cannot be considered sufficient to differentiate populations at species or subspecies level when comparative examination has been made of material from the whole range of the species.

O. infernalis was originally described from Japan. No locality was given but the species is known to extend from Kyushu island in the south to at least the central region of Honshu island in the north. Measurements for a series from Japan are given above (p. 129). The subspecies *O. infernalis amurensis* was a name coined by Ikonnikov for the unnamed variety '*O. infernalis* var?' from Amur described by Saussure (1884: 117). The varietal name *amurensis*, incorrectly attributed by him to Saussure, should therefore be considered as his own, as was correctly assumed by Bei-Bienko & Mishchenko (1951*b*: 577) when elevating the variety to subspecific status. However, because Ikonnikov attributed his name to Saussure he did not designate his material as types or place the words 'var. n.' after the name as he did elsewhere in the same paper when describing new taxa. In any case his material, originally housed in the 'Zoologischen Museum der Kais', Moscow University, is presumably lost. The unique male in Saussure's collection at Geneva is here regarded as the type and accordingly designated as the lectotype of *Oedaleus infernalis amurensis* Ikonnikov, 1911. Measurements of a series of specimens of both sexes from the type-locality are given above together with measurements of the lectotype (p. 129). Compared to Japanese specimens they are noticeably smaller though the ranges overlap. However, the shape, as judged by TL/PL and the length/depth ratio of the hind femur, is substantially identical.

Oedaleus manjius Chang, 1939 was described from material collected in Chekiang and Szechwan provinces of China. The measurements of a series collected at 1500 m in Szechwan and loaned to me by Dr A. B. Gurney (USNM, Washington) are given above (p. 130). The series was studied by Chang and one specimen (not measured) had been labelled '*Oedaleus wenchowensis* Chang, det. Chang 1936'. I am indebted to Dr Gurney for the following information:

'Chang's material, which had been borrowed here, was never returned from China, so that we do not have types or other material except what he named while in the United States, where he studied at Cornell University. In China he was at St. John's University, Shanghai, but whether anything of his remains there is unknown to us here. It is probable that he did not survive the war. My last word from him was in April 1939, at which time conditions there were very much upset. The name *Oedaleus wenchowensis* Chang which he placed on a label here in 1936 evidently applies to what he described in 1939 as *O. manjius*, the former just being a manuscript name of no permanent validity.'

Unfortunately Chang's diagnostic characters for *O. manjius* are unreliable since specimens from one locality exhibit great variation in minor details of the morphology of the head and pronotum and the colour of the hind tibiae and the ventral surface of the hind femora, all characters which he considered as conclusive in distinguishing his species from *O. infernalis*.

Oedaleus infernalis montanus Bei-Bienko, 1951 was described from material collected in 'Szechwan, Nan Shan Mts, and range of Burkhan-Budda'. The male only was described and distinguished by its author from other subspecies by the colour of the hind femora, by its small size, and by minute differences in the length of the 'median segments of antennae'. Of these characters only size is of any objective validity. The holotype was unavailable for study but the measurements of a paratype from Lifan are given above. Bei-Bienko & Mischenko (1951*b*: 577) gave the range of tegmen length of the type-series as 16·5–20·0 mm though the specimen measured here is actually smaller than this. Measurements of two females from near Lifan are given for comparison. One of these is very large indeed, suggesting that the Himalayan population is not composed exclusively of dwarf individuals, though doubtless specimens caught at high altitude have a tendency to small size and relatively short tegmina and hind femora, a well-known phenomenon in montane Acridoidea (Uvarov, 1977: 436). Tegmen length of Bei-Bienko's series has an almost identical range to that of the specimens studied by Chang mentioned above and overall there is consistency within the material from south-west China. From the measurements given it is evident that the TL/PL ratio is different for both sexes of the Szechuan population compared to the L. Khanka population which is essentially lowland-living (♂: $t = 6{\cdot}03$, $P < 0{\cdot}01$; ♀: $t = 7{\cdot}67$, $P \ll 0{\cdot}001$). A careful analysis of the effects of altitude on morphometrics in this species would be most interesting but at present there is no evidence of any genuinely geographically based variation worthy of subspecies status. In any case morphometric variation even within one population is so great that subspecies divisions based on only a few specimens from widely scattered localities are biologically meaningless.

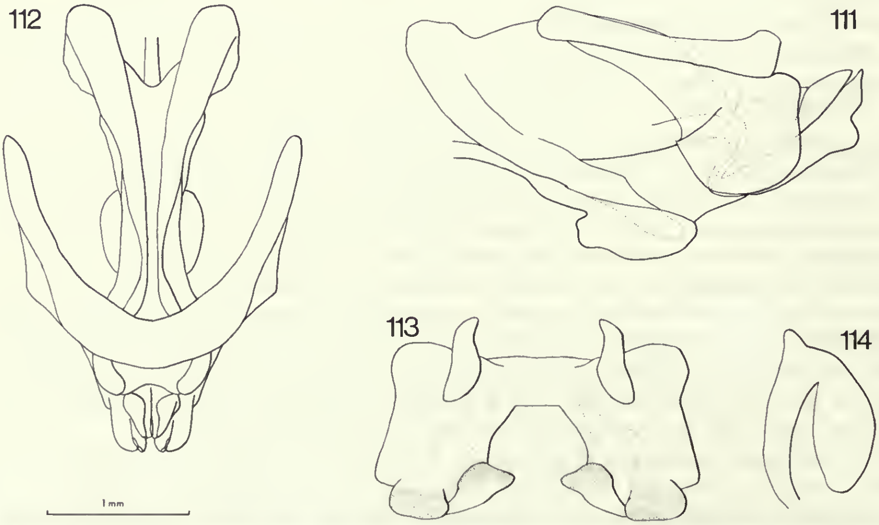
The original series of *O. infernalis* was stated by Saussure to be in Brunner's collection. There are today three specimens labelled as from Japan in the NM, Vienna. Of these the single male is designated as the lectotype, and the two accompanying females are designated as paralectotypes.

Oedaleus formosanus (Shiraki, 1910) **comb. n.**

(Figs 7, 38, 53, 111–114, 163)

Oedipoda formosana Shiraki, 1910: 89. NEOTYPE ♂, TAIWAN: Taikaizan (BMNH), here designated [examined].

♂. Integument finely rugulose and sparsely hairy. Antennae about one and a third times as long as head and pronotum together, flagellum with 19 segments. Fastigium of vertex longer than wide, narrowing to half maximum width anteriorly, concave, with raised margins; frons in profile flat, frontal ridge narrowed just below vertex and again just below median ocellus. Eyes nearly one and a half times as deep as wide; genae sparsely hairy. Pronotum tectiform, finely rugose and pitted; median carina arcuate, intersected by posterior sulcus; lateral lobes of pronotum sparsely covered with long hairs; hind margin nearly rectangular; lateral surface of meso- and metathorax sparsely hairy. Tegmen surpassing folded hind knees by less than one-quarter of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs about one and a half times as long as outer; apical tarsal segment three times as long as claw; arolium more than one third length of claw. Cerci



Figs 111–114 *O. formosanus*, genitalia. 111, endophallus and cingulum, lateral view; 112, same, dorsal view; 113, epiphallus; 114, spermatheca.

more than two and a half times as long as wide. Genitalia (Figs 111–113): cingular apodemes medium length, strongly curved, zygoma thickened; rami short, cingular and apical penis valves short, the latter with acute apices; subapical ventral process tumuliform; epiphallus long and broad with deeply arched bridge; lophi large, outer lobes wider than inner; anterior projections large, rounded, posterior projections rectangular.

General coloration brown, with darker brown markings. Head brown with oblique dark striations on genae and frons, vertex speckled. Pronotal X-marking forming a light area on shoulders of pronotum bounding dark medial area on dorsum; lateral surface of pronotum and meso- and metanotum with variable light and dark specks. Tegmen infuscate brown throughout except for irregular pale triangle on costal margin one-third along from base and transparent specks in apical half visible when wing is open. Hind wing fascia (Fig. 7) complete and fusing posteriorly with infuscate wing tip; basal area pale greenish yellow. Outer surface of hind femora with three oblique dark bands, inner surface with three transverse bands partially elided; interior ventral carina and ventral surface of hind femur scarlet; hind knees black; hind tibiae with thin black basal ring, otherwise coral to scarlet.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 53) narrow, almost triangular, strongly sclerotized, with curved apices. Spermatheca (Fig. 114) with apical diverticulum abruptly rounded apically, and with conical subapical diverticulum.

MEASUREMENTS (all known specimens)

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·82	3·94	4·89	18·2	12·91	2·98	4·35	3·71
Range	22·4–29·6	3·6–4·5	4·4–5·5	15·6–20·9	12·0–14·4	2·4–3·3	4·1–5·0	3·5–4·0
S.D.	2·337	0·292	0·365	1·754	0·833	0·287	0·312	0·156
n	6	7	7	6	7	7	7	6

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	34·34	5·94	7·16	23·97	17·74	4·25	4·17	3·34
Range	29·8–41·0	5·5–6·7	6·5–8·6	19·7–29·3	15·9–20·9	3·9–4·8	3·8–4·3	3·0 3·4
S.D.	4·725	0·487	0·944	3·950	2·15	0·376	0·231	0·207
n	4	4	4	4	4	4	4	4

AFFINITIES. *O. formosanus* appears to be most closely allied to *O. infernalis,* but is quite distinct by virtue of its dark coloration and the extensive shading of the hind wing (Fig. 7), both features which are common to many high altitude oedipodine grasshoppers.

MATERIAL EXAMINED

Oedaleus formosanus (Shiraki), neotype ♂, **Taiwan:** Taikeizan, 25.viii.1923 (*Shiraki*) (BMNH).

Taiwan: 1 ♀, Taikeizan, 25.viii.1923 (*Shiraki*) [labelled 'Oedaleus formosanus Shir. Cotyp.']; 1 ♂, 1 ♀, Daisuikutsu, 14.ix.1924 (*Shiraki & Sonan*) [♀ is labelled 'Oedaleus formosanus Shir. Cotyp.']; 2 ♀, Arisan, 2.vii.1947 (*Gressitt*) (CAS, San Francisco); 1 ♂, Arizan, 21.viii.1908 (ANS, Philadelphia); 3 ♂, Alishan, Chiayi Hsien, 1800 m, 11.ii–3.iii.1962 (*Yoshimoto*) (BPBM, Hawaii); 1 ♂, Arisan, 2130 m, 22.viii.1947 (*Gressitt*) (BPBM, Hawaii).

DISTRIBUTION (Fig. 163, and Biogeography section, p. 165). Known only from montane areas of Taiwan.

BIOLOGY. Unknown.

DISCUSSION. This species was not fully described by Shiraki (1910), probably as a result of an oversight, and it is known only from pl. 2, fig. 3 and the legend '*Oedipoda formosana* n. sp.'. In 1929, four specimens of this species were donated to the British Museum (Natural History) via the Commonwealth Institute of Entomology, and these were entered in the C.I.E. donations book on April 6th as four cotypes of *Oedaleus formosanus*. There are a number of problems posed by this situation. Firstly, only the two females actually bear manuscript labels identifying them as cotypes, though it is probable that in his correspondence with C.I.E. Shiraki described them all as cotypes. This cannot now be verified since all pre-war C.I.E. correspondence was pulped during World War II. The second problem is that specimens collected several years after the publication of a species cannot possibly be cotypes (or, in modern usage, syntypes). It is conceivable that they were designated in a later publication, but if so this cannot now be traced. What is clear is that by 1929 Shiraki had realized that his species was an *Oedaleus* and he labelled the specimens he sent to C.I.E. accordingly. However, since no publication of this combination is known, it is here given as a new combination. Presumably Shiraki had specimens before him when writing his 1910 paper which he intended to designate as types but this material is now lost. Dr Syoziro Asahina has kindly checked Shiraki's collection at Hokkaido University, Sapporo, and he informs me that there is no named specimen of *Oedipoda formosana*. For this reason, and to establish the identity of the species, one male from Shiraki's later series is here designated as neotype.

Oedaleus interruptus (Kirby 1902)

(Figs 13, 26, 46, 115–118, 152)

Chortoicetes interruptus Kirby, 1902*a*: 232. LECTOTYPE ♂, SOUTH AFRICA: Transvaal (BMNH), here designated [examined].

Oedaleus interruptus (Kirby) Uvarov, 1925: 275.

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum 20-segmented. Fastigium of vertex subtriangular, longer than wide with well-defined margins, narrowing anteriorly to one-third of maximum width. Frons in profile slightly convex. Frontal ridge slightly expanded dorsal to median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum low tectiform, median carina arcuate, blade-like, not intersected by posterior sulcus. Posterior margin of pronotum acutangular to rectangular. Tegmen surpassing folded hind knees by one-fifth to one-third of hind femur length. Hind tibia with 11–12 inner and 11–13 outer spines. Inner apical spurs about one and a half times as long as outer. Apical tarsal segment about twice length of claw, arolium half length of claw. Cerci elongate, more than two and a half times as long as wide. Genitalia (Figs 115–117): cingular apodemes short, of medium thickness; rami long, slender; cingular and apical penis valves short, subapical ventral process large; epiphallus rectangular, bridge narrow, inner lobes of lophi three times as wide as outer lobes.

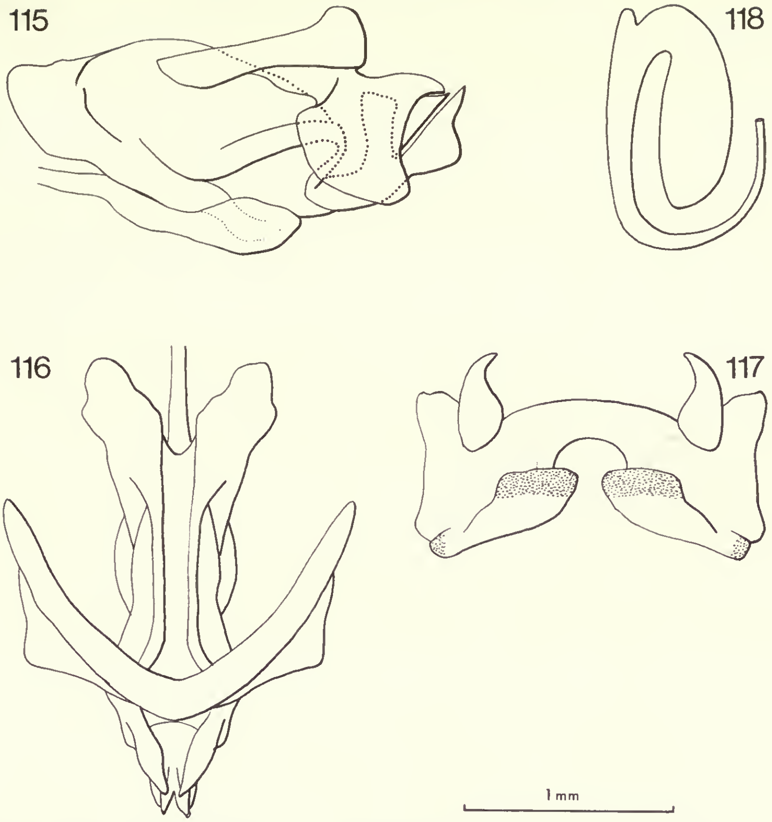
General coloration variable, brown, with lighter brown or green markings on vertex, frons, genae, pronotum, dorsal and lateral surface of folded tegmina and dorsal surface of hind femora. Pale X-marking of pronotum thin and distinct (♀ Fig. 26). Tegmen infuscate brown or brown and green in basal half with four pale transverse bands one-quarter, one-third, one-half, and three-fifths along from base; apical two-fifths clear with variable smoky patches. Hind wing fascia (Fig. 7) narrowly interrupted between second cubitus and first anal vein, or more widely, reaching margin of wing posteriorly; wing tip sometimes slightly infuscate, basal area of wing pale yellow. Hind femur with two transverse brown bands on external upper marginal area and one longitudinal brown streak on external medial area; ventral surface of hind femur suffused (often indistinctly) with rose pink. Hind tibia basally pale straw, otherwise brown suffused with pink. Hind knees brown or greenish.

♀. Ventral ovipositor valves (Fig. 46) moderately sclerotized, slender, Spermatheca (Fig. 118) with finger-like subapical diverticulum.

MEASUREMENTS (all available material)

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·18	3·63	4·49	17·28	12·57	3·2	3·93	3·87
Range	21·1– 25·1	3·3– 4·0	4·0– 5·2	15·4– 19·1	11·0– 13·6	2·8– 3·6	3·8– 4·2	3·5– 4·3
S.D.	1·06	0·195	0·356	1·047	0·786	0·230	0·120	0·234
n	9	11	10	11	10	10	10	10



Figs 115–118 *O. interruptus*, genitalia. 115, endophallus and cingulum, lateral view; 116, same, dorsal view; 117, epiphallus; 118, spermatheca.

Females

Mean	27·68	4·64	5·08	20·08	13·82	3·53	3·92	3·97
Range	25·1–31·6	4·2–5·0	4·1–5·9	17·9–22·9	12·6–15·9	3·1–4·0	3·8–4·1	3·6–4·5
S.D.	2·052	0·240	0·430	1·566	0·998	0·267	0·111	0·262
n	12	13	12	13	12	12	12	12

AFFINITIES. *O. interruptus* is probably most closely related to *O. carvalhoi* with which it shares the characteristics of very fine X-markings on the pronotum, red hind tibiae and undersides of hind femora, and incomplete wing band. It is easily distinguished by its smaller and slenderer appearance and the acutely angled pronotal hind margin, an unusual feature in *Oedaleus*.

MATERIAL EXAMINED

Chortoicetes interruptus Kirby, lectotype ♂, **South Africa:** Transvaal, Pretoria (*Distant*) (BMNH).

South Africa: 1 ♂, 4 ♀, Transvaal, Pretoria (*Distant*) (including 1 ♀ paralectotype of *Chortoicetes interruptus* Kirby); 1 ♀, T., Krugersdorp, 22.xii.1902 (*Hamm*) (UM, Oxford); 1 ♂, T., Johannesburg (*Cregoe*); 1 ♂, Orange Free State, Harrismith, ii.1927 (*Turner*); 1 ♀, O.F.S., Gum Tree, ii.1932; 4 ♂, 9 ♀, O.F.S., Bloemfontein, 13.iv.1951 (*Botha*) (COPR, London); 1 ♀, Orange R. Colony (*B-Hamilton*); 1 ♂, 1 ♀, Cape Province, Grahamstown, 23.ii.1955 (*Greathead*); 2 ♂, C.P., Drakensburg Mts, Giant's Castle, 1957 (*Jago*); 1 ♀, C.P., 35·4 km W. of Cofimvaba, 940 m, 14.iv.1958 (*Ross & Leech*) (CAS, San Francisco); 1 ♀, C.P., Cape of Good Hope (*Brady*) (MHN, Geneva); 1 ♀, C.P., Cape of Good Hope (*Peringuey*) (MHN, Geneva); 1 ♂, 1 ♀, C.P., Bot River, xii.1930 (*Key*) (ANIC, Canberra).

Distribution (Fig. 152, and Biogeography section, p. 156). Known only from eastern montane areas of South Africa.

Biology. Unknown. There is one report of damage to wheat at Bloemfontein (13.iv.51, *D. H. Botha*) recorded in the COPR collection index: 'The edges of the fields were severely damaged and in some cases had to be reploughed and resown. The fliers mostly roosted in grass outside the wheat fields and flew into them daily to feed on the green wheat'.

Discussion. Kirby described *Chortoicetes interruptus* from material collected by Distant at Pretoria. Only one male and one female were referred to the new species. Kirby misidentified one further male and three females with identical data to the syntypes. Accordingly the single named male is designated lectotype and the female paralectotype. The remaining specimens are excluded from the paralectotype series.

Oedaleus instillatus Burr, 1900
(Figs 12, 33, 56, 119–123, 156)

Oedaleus instillatus Burr, 1900: 39. LECTOTYPE ♂, Somali Republic (UM, Oxford), here designated [examined].

Redescription. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two-fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at and narrowed below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin rectangular to acutangular. Tegmen surpassing folded hind knees by one-third to one-half of femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a half times claw length; arolium two-fifths of claw length. Cercus one and four-fifths as long as wide. Genitalia (Figs 119–123): cingular apodemes of moderate thickness and curvature; rami fully developed with cingular and apical penis valves short; subapical ventral process large; epiphallus rectangular, inner and outer lobes of lophi small, subequal; anterior projections rounded, acute; posterior projections obtusangular.

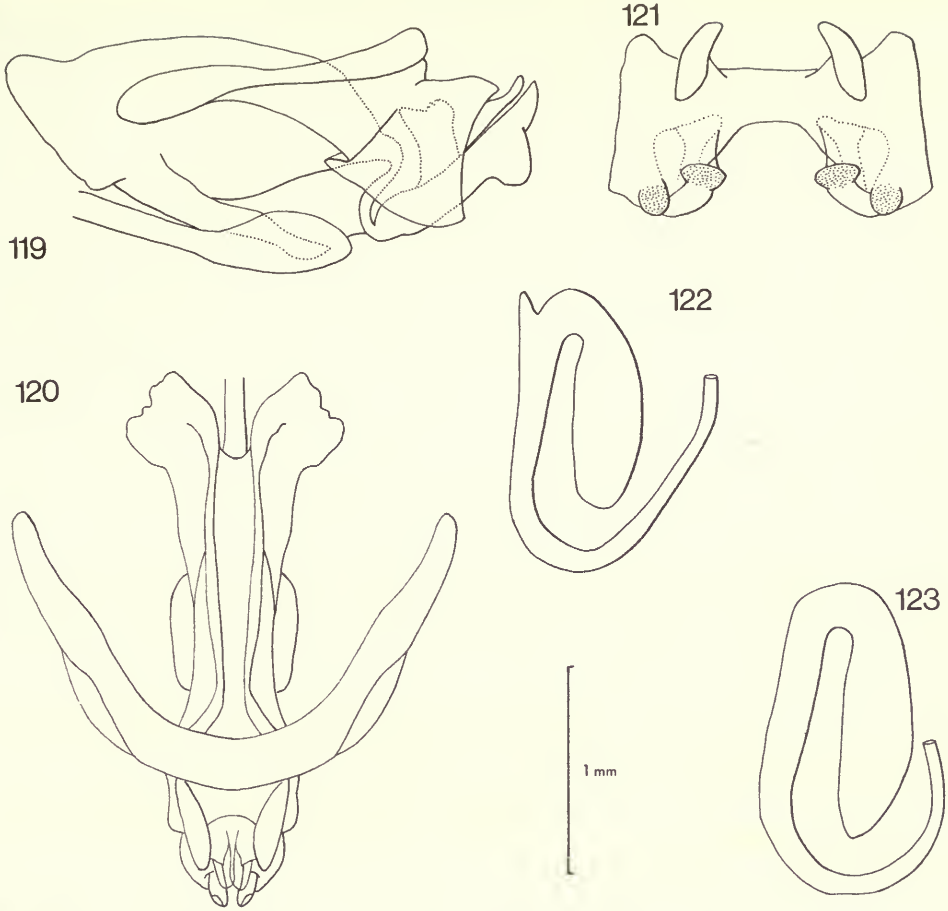
General coloration variable, brown, with lighter brown (or, rarely, pale green) markings on frons, vertex, genae, pronotum, and dorsal surface of folded hind tegmina and hind femora. Tegmen infuscate in basal two-thirds with three pale transverse bands situated one-third, one-half and two-thirds along from base, commencing from costal margin. Hind wing fascia (Fig. 12) complete, reaching hind margin of wing, basal area pale yellow, wing tip infuscate. Hind femur with three oblique transverse bands on external medial and upper marginal areas; internal surface with basal pair of bands elided to form dark area; ventral surface pale red; hind knees dark brown, hind tibia with dark basal ring, thick subbasal pale area, otherwise pale red.

♀. Hind femur and tibia with very pale red pigment often appearing light brown. Ventral ovipositor valves (Fig. 56) elongate, moderately sclerotized, with exterior margin deeply incurved. Spermatheca (Fig. 122) with or without a short finger-like subapical diverticulum.

Measurements
Sample from Kenya: El Wak, 2°47′N, 40°55′E, 5.xii.1944 (*Kevan*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26·97	3·56	4·59	18·97	11·9	3·01	4·16	4·14
Range	23·8–	3·3–	4·2–	17·5–	11·2–	2·8–	3·7–	3·6–
	27·6	3·9	5·3	20·7	12·8	3·2	6·9	4·6
S.D.	7·045	0·142	0·287	0·82	0·411	0·125	0·795	0·259
n	28	29	26	29	14	14	14	25



Figs 119–123 *O. instillatus*, genitalia. 119, endophallus and cingulum, lateral view; 120, same, dorsal view; 121, epiphallus; 122, spermatheca.

Females

Mean	32·61	4·90	5·77	24·11	15·15	3·83	3·95	4·20
Range	28·2–37·3	4·3–5·8	4·6–6·9	22·0–27·4	12·9–18·0	3·3–4·5	3·8–4·1	3·6–4·7
S.D.	1·946	0·339	0·589	1·429	1·404	0·328	0·106	0·316
n	25	24	25	25	14	14	14	25

AFFINITIES. *O. instillatus* is allied to *O. rosescens* and *O. obtusangulus* on the basis of its epiphallus morphology (Fig. 121), the lophi being small and of nearly equal size. It also shares with them its sombre coloration, green forms being relatively rare. This reflects the open dry habitats favoured by these species.

MATERIAL EXAMINED

Oedaleus instillatus Burr, lectotype ♂, **Somali Republic:** W. Somaliland, 16.iv.–7.viii.1895 (*Peel*) (UM, Oxford).

In addition to the lectotype, 468 specimens were examined from the following localities. **Somali Republic:** 1 ♀, W. Somaliland, 16.iv.–7.viii.1895 (*Peel*) (UM, Oxford) (paralectotype of *Oedaleus instillatus* Burr); Las Anod; Belet Uen; Debifrad; Adenival; 11·3 km N. of Bulo Burti; 9·7 km N. of Bulo Burti; nr Borama, 1350 m; 37 km N. of Borama, 10°03′N, 43°12′E; Hargeisa, locust camp; Hargeisa Tug; between Hargeisa and Mandera; Derkengenyu; Mijertein, Domo; Ischia Baidoa; El Rago; Burao; El Afwein, N. Region; Wud Wud, 80·5 km NE. of Bohotle; between Mait and Las Khoreh, Haded Plain; Bohotleh; Welo, 09°28′N, 48°55′E; Afmadu; Haud, 8°29′N, 45°34′E, 750 m; N. Region, El Donfar, 10°40′N, 49°05′E; Hudin area, 09°10′N, 47°30′E; Erigavo scarp, 750 m; Mogadiscio, 5.vi.55; Bawn; Au Barre, 09°47′N, 43°13′E; Mijertein, nr Bender Beila. **Djibouti:** Dia forest, 64·4 km N. of Tadjura. **Ethiopia:** Ogaden, Wardere; Dire Daoua; Kobo; El Oha; Wallo, Yeju escarpment; Ogaden, nr Scillare; nr Ogaden, Argheile, 300 m, 05°10′N, 42°05′E; Dua Parma R., 1000 m; Erer Hotel; Harerge Province, Erer to Urso road, 12·1 km E. of Erer; Harerge Pr., 0·6 km E. of Erer, 1200 m. **Kenya:** El Wak, N.F.D.; Wajir distr., War Olia, 02°20′N, 40°33′E; Makindu; Voi; Machakos Hills; Samburu distr., Wamba, 00°58′N, 37°19′E; Madagheddi, Mandera distr., 03°43′N, 41°39′E; Mandera distr., Damassa, 03°09′N, 41°20′E; Kima; Magadi; Nairobi, Langata forest; 03°25′N, 40°12′E; Athi; Marsabit; Kindaruma, 00°47·5′S, 37°39·5′E; 6 km E. of Makutano, 02°31′S, 37°34·5′E; 16 km E of Makutano, 02°31′S, 37°40′E; Chyulu hills, 02°32′S, 37°46′E, 02°34′S, 37°49′E, 02°38·5′S, 37°51·5′E; Hola, 01°30′S, 40°00′E; Garissa to Thika, 00°47′S, 38°45′E; Selengai; Ulu; Samburu distr.; Giaxi, 00°01·5′N, 37°46′E; 9 km N. of Ishiara, 00°24·5′S, 37°51′E; Mt Marsabit, 7 km N. of Loglogu, 02°04′N, 37°54′E, 690 m; Meru National Park, 00°13′N, 38°05′E, 750 m; Meru Nat. Pk, 00°11′N, 38°04′E, 720 m; Meru Nat. Pk, site of old game lodge on Rojoweru R., 00°08′N, 38°16′E, 450 m; Meru Nat. Pk, 00°05′N, 38°16·5′E, 510 m; Meru Nat. Pk, Simba Lookout, 00°08′N, 38°09′E, 630 m; about 5 km W. of Ishiara town, 00°27′S, 37°45′E, 1050 m; approx. 3 km E. of Taru village, 03°45·5′S, 39°10′E, 330 m; 17 km NE. of Mambeala Rock, on road from Nguni to Kora, 00°20′S, 38°32′E, 540 m approx.; Mambeala Rock, road from Nguni to Kora, 00°26′S, 38°26′E, 720 m; 3 km SW. of Mambeala Rock, 00°27′S, 38°25′E, 720 m; Mt Marsabit, about 1 km from main road on short cut to L. Paradise, 02°16′N, 37°54′E, 1260 m; on road from Samburu to Marsabit, 101 km N. of Archer's Post, and 1 km S. of Merille R. bridge, 01°24′N, 37°43′E, 570 m; 17 km N. of Loglogu, at side of main road, 02°09′N, 37°53′E, 900 m; Salt Lick Lodge, 03°33′S, 38°13′E, 870 m; game area owned by Taita Hills Lodges, 03°32′S, 38°14′E, 900 m; Taita Hills Lookout, Mukiaio; Buffalo Springs Res., 00°33′N, 37°38′E, 15.vi.75; Ndetani, on road from Nguni to Kora (meeting place of five tracks), 00°35′S, 38°22′E, 720 m; Samburu distr., Varaguers Valley, E. of Wamba. **Tanzania:** Dodoma; Mkomasi station, 97 km W. of Amani; Kibwezi, Ukamba, 900 m; Meru, Nieder.

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). Widely distributed and common throughout the drier areas of eastern Africa.

BIOLOGY. Almost nothing is known of the biology of this common species. From label data it is apparent that adults may be seen at all times of the year. One hopper has been collected in January and one copulation observed in May. It is notable that specimens are rarest in March and July, both months of low rainfall, the latter also having lowest temperatures. Peak numbers have been collected in May and November, in each case one month after the two months of peak rainfall (Griffiths, 1972: 139). It is clear that there are at least two generations corresponding to these peaks and perhaps more in years of above-average rainfall. There is one record of night-flying 'swarms' of *O. instillatus* observed at El Wak in NE. Kenya, on 5.xii.1944 between 20.00 and 22.00 h (Kevan & Knipper, 1955: 312) but no details of density or behaviour were given. The measurements given are for a series from this swarm.

DISCUSSION. Burr described *O. instillatus* from one male and one female syntype. The male is here designated lectotype and the female paralectotype.

Oedaleus obtusangulus Uvarov, 1936

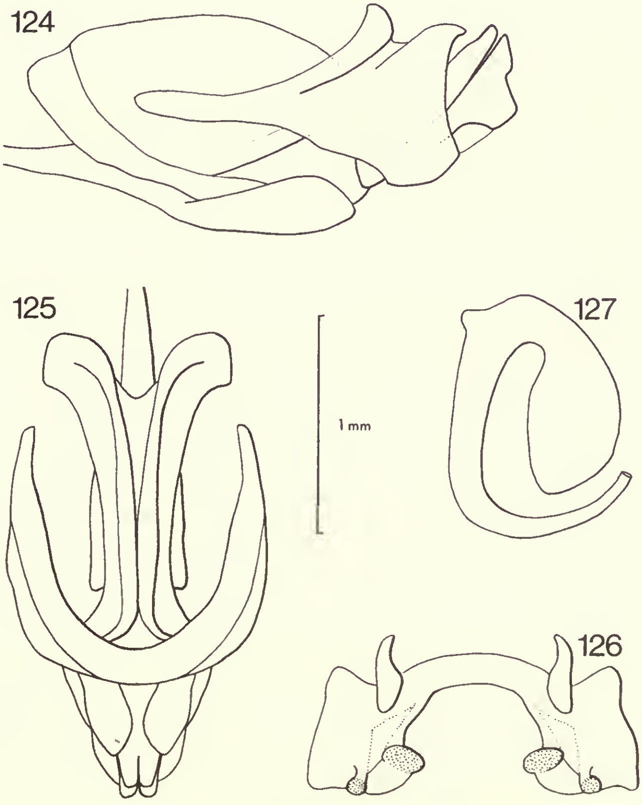
(Figs 3, 35, 55, 124–127, 156)

Oedaleus obtusangulus Uvarov, 1936: 542. Holotype ♀, SAUDI ARABIA (BMNH) [examined].
Oedaleus villiersi Chopard, 1950: 139. Holotype ♀, NIGER (MNHN, Paris) [examined]. **Syn. n.**

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium of vertex longer than wide narrowing to half maximum width anteriorly, concave with raised margins; frons in profile slightly convex; frontal ridge constricted at vertex, slightly widened between antennal bases, constricted below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform, rugose, with deep sulci; median carina arcuate, hind margin rectangular to obtusangular. Tegmen surpassing folded hind knees by one-half to one-third of length of hind femur. Hind tibia with 11 inner and 10–11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice length of claw; arolium less than half length of claw. Cerci twice as long as basal width. Genitalia (Figs 124–126): cingular apodemes long, strongly curved; rami well developed; cingular and apical penis valves short; subapical ventral process large; epiphallus elongate trapezoidal with thin arched bridge; inner lobes of lophi small, twice as wide as outer lobes; anterior projections large, rounded acutangular; posterior projections smaller, rounded acutangular.

General coloration greyish brown with lighter markings on frons, genae, pronotum, tegmina and hind femora. Tegmen infuscate in basal half, with two irregular pale transverse bands extending from costal margin, first band one-third along from base, reaching at least to subcostal vein, sometimes to second cubitus posteriorly; second band half way along wing, reaching first cubitus posteriorly. Apical third of tegmen clear with variable degree of infuscate speckling. Hind wing fascia (Fig. 3) variable in emphasis, widely but variably interrupted around first cubitus, reaching hind margin of wing posteriorly; basal area pale yellow or colourless. Hind femur with three variable transverse markings on external and internal upper marginal area extending indistinctly obliquely forward across external medial area; inner and ventral surfaces of hind femur straw-coloured; hind tibia with dark basal ring, subbasal pale area, otherwise straw-coloured.

♀. Ventral ovipositor valves (Fig. 55) elongate, weakly sclerotized, laterally excavated; basivalvular sclerite smooth. Spermatheca (Fig. 127) with short rounded apical diverticulum and very short subapical diverticulum.



Figs 124–127 *O. obtusangulus,* genitalia. 124, endophallus and cingulum, lateral view; 125, same, dorsal view; 126, epiphallus; 127, spermatheca.

MEASUREMENTS

Sample from Saudi Arabia: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	21·52	3·32	3·85	15·62	10·08	2·72	3·71	4·08
Range	18·6–24·0	2·9–3·5	3·5–4·3	13·7–17·5	9·1–11·6	2·2–3·1	3·5–4·0	3·6–4·6
S.D.	1·339	0·171	0·280	1·007	0·672	0·202	0·123	0·269
n	20	21	21	20	21	21	21	20
Females								
Mean	28·43	4·62	5·21	20·44	13·61	3·59	3·79	3·93
Range	25·2–32·9	4·1–5·3	4·6–6·1	18·1–23·9	11·9–15·5	3·1–4·0	3·5–4·1	3·6–4·3
S.D.	2·079	0·381	0·393	1·474	0·976	0·236	0·147	0·164
n	16	16	16	16	16	16	16	16

Sample from Niger: Aïr (all available material of '*villiersi*').

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	23·1	3·4	4·2	17·0	10·9	2·8	3·8	4·1
Paratype ♂	22·0	3·2	3·8	16·4	9·7	2·8	3·5	4·3
Paratype ♂	23·8	3·4	4·1	17·8	10·4	2·7	3·8	4·3
Paratype ♀	28·7	4·8	5·4	20·9	13·4	3·8	3·5	3·9
Holotype ♀	28·1	4·6	5·2	20·4	13·6	3·6	3·7	3·9

AFFINITIES. *O. obtusangulus* is most closely allied to *O. instillatus* and *O. rosescens* on the basis of general shape and colour and in particular the morphology of the epiphallus, which in all three species has small inner and outer lobes of equal size.

MATERIAL EXAMINED

Oedaleus obtusangulus Uvarov, holotype ♀, **Saudi Arabia:** Buraiman, 17.ii.1929 (*Philby*) (BMNH). *Oedaleus villiersi* Chopard, holotype ♀, **Niger:** Aïr, Tésuar, viii.1947 (*Chopard*) (MNHN, Paris).

Saudi Arabia: 3 ♂, 2 ♀, Asir, Wadi Hali, 18°45′N, 41°55′E, 300 km, 9–10.i.1948 (*Popov*); 1 ♂, 1 ♀, Wadi Harub, 17°10′N, 42°50′E, 1.i.1947 (*Popov*); 1 ♀, Wadi Jowra, 17°15′N, 43°00′E, 30.xii.1946 (*Popov*); 1 ♀, Lahawash, foothills NE. of Sabiya, 150–240m, 18.i.1950 (*Tillin*); 1 ♂, Buraiman, nr Jeddah, 17.i.1947 (*Popov*); 1 ♂, Hawi valley, 20.v.1936 (*Philby*); 6 ♂, 3 ♀, Lodar, 800 m, 16.v.1967 (*Guichard*); 2 ♂, Seil el Kebir, 23.iii.1969 (*Popov*); 1 ♂, Aqiq–Baha, crops, 3.vi.1969 (*Popov*); 1 ♀, Baha, 7.vi.1969 (*Popov*); 1 ♀, 2 nymphs, Aqiq, 2.vi.1969 (*Popov*); 3 ♂, 2 ♀, Hada, *Acacia* bush, 1700 m, 4.v.1969 (*Popov*); 1 ♀, Upper Wadi Alahsiba, Tihama, 10.ii.1962 (*Popov*); 1 ♂, Sab[i]ya, 17°10′N, 72°40′E, iii.1945 (*Waterston*). **Yemen:** 1 ♀, Hodeidah, locust research station [actual site of collection unknown]. **Niger:** 1 ♂, Tarrouadji, 900 m, viii.1947 (*Chopard*) (MNHN, Paris); 2 ♂, Aïr, Irabellaben, ix.1947 (including allotype ♂ of *Oedaleus villiersi* Chopard) (MNHN, Paris); 1 ♂, Aïr, 100 km N. of Agadez towards In Guezzam, 25.viii.1967 (*Popov*).

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). This species has a relict montane distribution in the western Sahara and south-west Arabia.

BIOLOGY. Unknown.

DISCUSSION. The measurements given above indicate that the few known specimens of *O. villiersi* fall well within the range of size of *O. obtusangulus*. In all other respects the two separated populations appear to be morphologically identical. Chopard was probably unaware of the Arabian species previously described by Uvarov when he described *O. villiersi*.

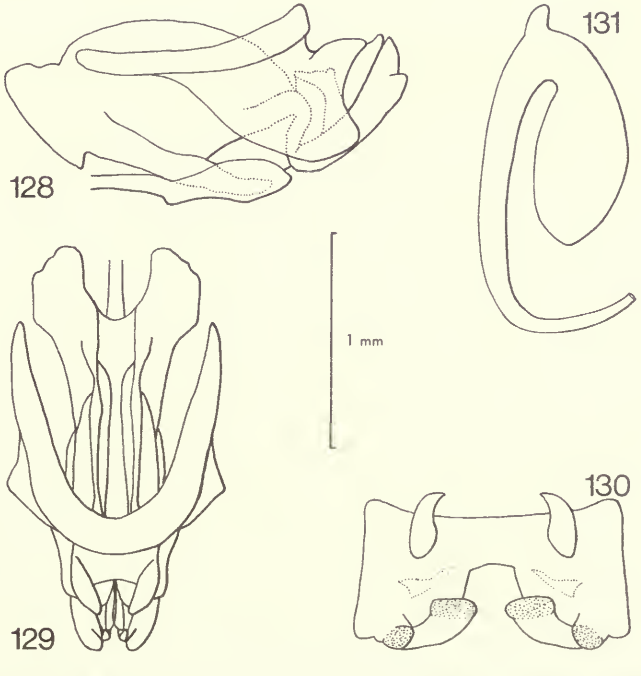
Oedaleus rosescens Uvarov, 1942
(Figs 4, 31, 54, 128–131, 157)

Oedaleus rosescens Uvarov, 1942: 582. Holotype ♂, INDIA (BMNH) [examined].

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a half times as long as head and pronotum together; flagellum with 22 segments. Fastigium of vertex much longer than wide, concave, narrowing to about half of maximum width anteriorly, with well-defined margins; frons in profile convex; frontal ridge slightly expanded at median ocellus. Eyes 1·3 times as deep as wide. Pronotum low tectiform; median carina arcuate, barely intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing hind knees by about one-third of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 128–130): cingular apodemes long and strongly curved; rami well developed with short cingular valves and apical penis valves; subapical ventral process small; epiphallus rectangular with narrow thick straight bridge angled within; inner lobes of lophi one and a half times wider than outer lobes; ancorae small; anterior and posterior projections rounded rectangular.

General coloration reddish brown with lighter brown markings on frons, genae, pronotum, tegmina and hind femora. Tegmen infuscate brown in basal half, with irregular pale transverse band extending from costal margin to first cubitus posteriorly, situated one-third along from base, second transverse band reaching first cubitus about half way along wing; apical third of tegmen clear with variable brown speckling. Hind wing fascia (Fig. 4) complete, slightly sigmoid, reaching hind margin of wing; basal area of wing pale pink. Hind femur with three indistinct transverse dark markings on external upper marginal area. Internal lateral surface of hind femur black in basal half with black transverse band one-third back from apex; ventral surface of hind femur pink, hind knee internally black; hind tibia with dark basal ring, subbasal pale area, otherwise pale pink.

♀. Ventral ovipositor valves (Fig. 54) short with strongly curved apices. Spermatheca (Fig. 131) with apical diverticulum rounded, with short subapical diverticulum.



Figs 128–131 *O. rosescens*, genitalia. 128, endophallus and cingulum, lateral view; 129, same, dorsal view; 130, epiphallus; 131, spermatheca.

MEASUREMENTS (all available specimens)

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	22·2	3·24	3·63	16·31	10·39	2·94	3·55	4·47
Range	20·6– 24·0	3·0– 3·6	3·4– 4·0	15·2– 17·9	9·7– 11·2	2·6– 3·2	3·5– 3·7	4·3– 4·6
S.D.	1·202	0·178	0·213	0·912	0·516	0·177	0·09	0·083
n	8	8	7	8	8	8	8	7

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27·96	4·41	4·77	20·46	13·37	3·79	3·53	4·31
Range	25·9– 29·2	4·0– 4·7	4·4– 5·0	18·6– 21·8	12·4– 14·0	3·4– 4·0	3·36– 3·69	4·06– 4·69
S.D.	1·154	0·218	0·202	1·083	0·647	0·212	0·125	0·204
n	7	8	8	7	8	8	8	7

AFFINITIES. *O. rosescens* is most closely allied to *O. instillatus* and *O. obtusangulus* on the basis of general shape and coloration and more specifically the epiphallus shape (Fig. 130). It is, however, quite distinct by virtue of the continuous fascia (Fig. 4) and pink basal area of the hind wing.

MATERIAL EXAMINED

Oedaleus rosescens Uvarov, holotype ♂, **India:** Rajasthan, Nokh, 1.viii.1937 (BMNH).

India: 4 ♂, 4 ♀, nr Bikaner, Udramsar, 20.viii.1963 (*Popov*); 2 ♀, nr Bikaner, viii.1963 (*Popov*); 1 ♂, Rajasthan, nr Barmer, Cho[h]tan, 26.viii.1959 (*Flower*); 1 ♀, Rajasthan, Jaiselmer [Jaisalmer], sandy hillsides with coarse grass, 8.ix.1959 (*Flower*); 1 ♂, Rajasthan, Jodhpur, 15.ix.1959 (*Flower*). **Pakistan:** 1 ♀, Khewra, Salt Range, from green grass and green trees, 24.ix–x.1930 (*Hora & Pruthi*) (paratype of *Oedaleus rosescens* Uvarov); 1 ♂, Landhi, on grass, 7.x.1975 (*Bashir*).

DISTRIBUTION (Fig. 157, and Biogeography section, p. 163). NW. India and NE. Pakistan.

BIOLOGY. Unknown.

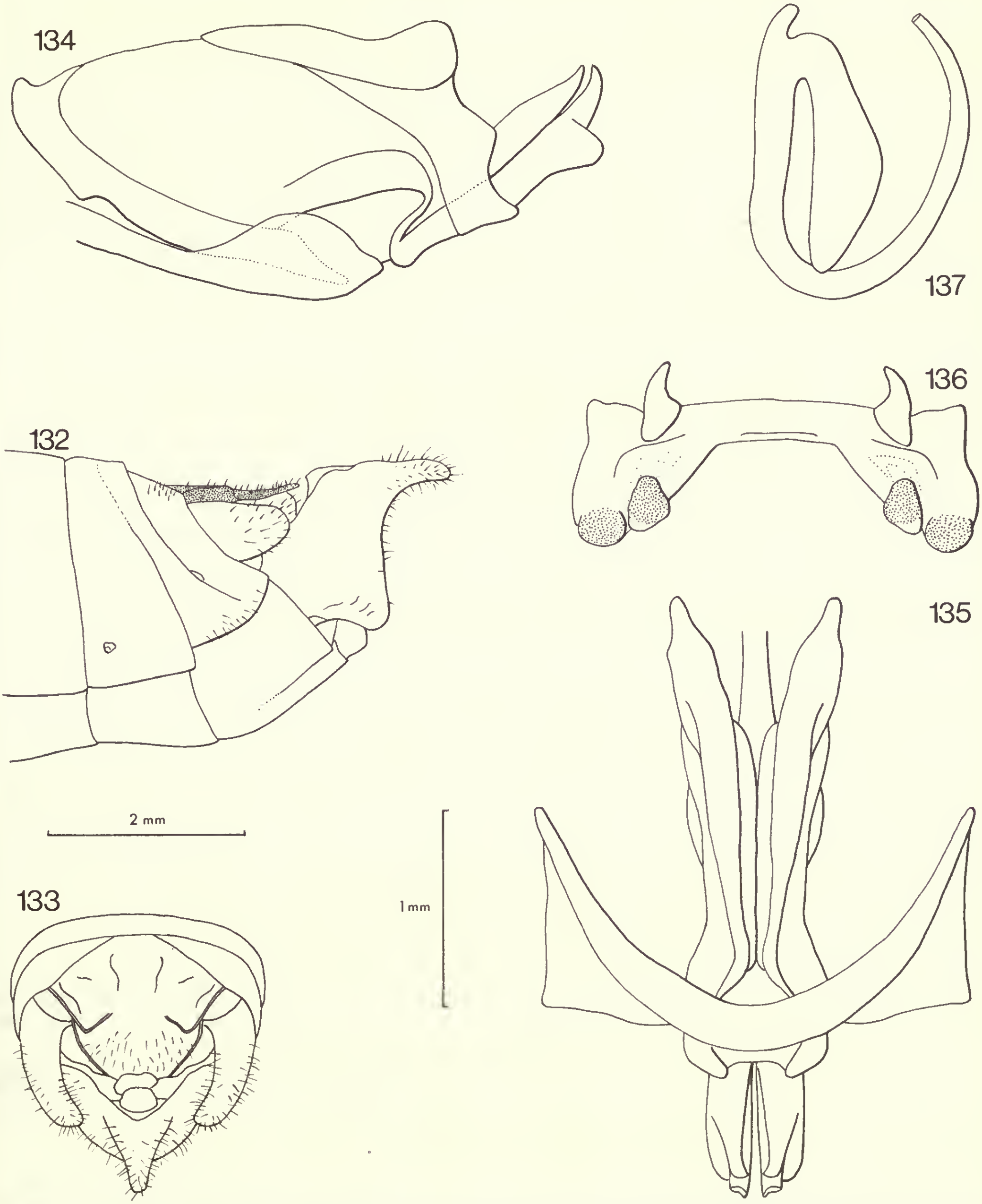
Oedaleus miniatus Uvarov, 1930
(Figs 16, 32, 59, 132–137, 156)

Oedaleus miniatus Uvarov, 1930*a*: 177. Holotype ♀, SOMALI REPUBLIC (BMNH) [examined].

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together, distinctly flattened, ensiform; flagellum with 22 segments. Fastigium of vertex longer than wide, concave, with well-defined lateral carinae, narrowing to one-third of maximum width anteriorly; frons in profile flat or slightly concave with projecting angle between frons and vertex; frontal ridge strongly narrowed just ventral to fastigium, expanded at and slightly constricted ventral to median ocellus. Eyes about one and a half times as long as wide. Pronotum tectiform, strongly rugose; median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal X-marking placed on narrow raised ridges; hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one-third of length of hind femur. Hind tibia with 11–13 spines inside and out; inner apical spurs about twice as long as outer; apical tarsal segment twice length of claw; arolium less than one-third length of claw. Cerci twice as long as basal width; subgenital plate with an acute dorsal posterior process (Figs 132, 133). Genitalia (Figs 132–136): cingular apodemes short, thin crescent-shaped, obtusely curved; rami short, reduced, with apices of cingular valves and apical penis valves long and exposed, the latter with acute flattened chisel-like tip and pronounced subapical ventral processes; epiphallus short and wide, with broad, thin, flat bridge, lophi with inner and outer lobes small and nearly of equal size; ancorae small; anterior projections small, rectangular; posterior projections obsolete.

General coloration variable, brown, with lighter brown or green markings on frons, vertex, genae and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half (Fig. 32). Tegmen infuscate brown in basal half with irregular pale transverse band on costal margin, reaching second anal vein posteriorly, situated one-third along from base, continuous when folded with light band on hind femur;

secondary light band between half and two-thirds along from base sometimes visible. Hind wing fascia (Fig. 16) complete, angled at dividing vein, spreading towards base and tip of wing along costal margin, basal area of wing bright scarlet, apical portion of wing slightly clouded. Outer surface of hind femora with three oblique transverse dark bands separated by lighter areas; interior surface with three transverse brown bands partially elided; interior ventral carina and ventral surface of hind femur orange-red; hind knees blackish, tibiae with incomplete narrow dark basal ring, subbasal wide pale ring, otherwise orange-red.



Figs 132–137 *O. miniatus,* genitalia. 132, apex of male abdomen, lateral view; 133, same, dorsal view; 134, endophallus and cingulum, lateral view; 135, same, dorsal view; 136, epiphallus; 137, spermatheca.

♀. Frons in profile concave to convex; head large. Pronotum rugose, warty. Tegmen shorter, just surpassing hind knees, narrowing towards apex; costal margin subbasally expanded. Hind wing scarlet, faded to salmon pink in some specimens, with dark fascia almost obsolete on small specimens. Hind femora with interior ventral carina suffused with orange-red; hind tibiae orange. Ventral ovipositor valves (Fig. 59) with weakly sclerotized apices. Spermatheca (Fig. 137) with apical diverticulum tapering proximally and distally, and with short finger-like subapical diverticulum.

MEASUREMENTS

Sample from Kenya: Hola, 1°30′S, 40°00′E (*I. A. D. Robertson*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25·67	3·88	5·26	18·36	12·47	3·63	3·44	3·51
Range	23·3– 27·9	3·5– 4·4	4·5– 6·2	16·6– 20·1	10·9– 14·0	3·1– 4·1	3·3– 3·8	3·1– 3·8
S.D.	1·465	0·265	0·534	1·078	0·884	0·272	0·126	0·219
n	10	11	11	10	11	11	11	10

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28·1	6·08	7·1	18·29	15·01	4·58	3·28	2·58
Range	26·4– 29·2	5·7– 6·5	6·7– 7·6	17·2– 19·0	14·4– 16·0	4·4– 4·8	3·1– 3·5	2·5– 2·7
S.D.	1·267	0·309	0·382	0·763	0·621	0·168	0·156	0·097
n	5	5	5	5	5	5	5	5

AFFINITIES. *O. miniatus* is most closely allied to *O. nadiae,* under which species the principal similarities and differences are discussed. The unique features of this species include the very wide epiphallus (Fig. 136) and the curiously elongated subgenital plate (Figs 132, 133). The female possesses the least sclerotized ovipositor valves of any member of the genus, which suggests some ecological difference in oviposition between this species and its near relatives. Conceivably egg pods are deposited among the roots of vegetation clumps rather than in the more resistant soil. This, however, is merely a hypothesis. The small equal-sized lobes of the epiphallic lophi suggest a tenuous link between *O. miniatus* and *O. nadiae* on the one hand, and the *obtusangulus-rosescens-instillatus*-group on the other. However, it is clear that *O. miniatus* has undergone a long period of evolutionary divergence from the main stem of *Oedaleus.*

Uvarov (1930*a*: 177) felt that *O. miniatus* might merit a separate genus, but incorrectly allied it to *O. carvalhoi,* to which it is not closely related. With the discovery of *O. nadiae,* an intermediate species between *O. miniatus* and the rest of the genus, there seems less reason to erect a new genus for the latter.

MATERIAL EXAMINED

Oedaleus miniatus Uvarov, holotype ♀, **Somali Republic:** Shimba Beris, Surud range, 10°54′N, 47°12′E, 2025 m, 17.xii.1929 (BMNH).

Somali Republic: 1 ♀, Beles Gogani, 01°30′N, 41°40′E, 30.ix–6.xii.1954 (*Greathead*). **Kenya:** Hola (Galole), Tana R. distr., 01°30′S, 40°00′E, 70 m, 11.vii.1972 (*Robertson*); 10 ♂, 5 ♀, same data, 29.xii.1972.

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). Known only from the Somali Republic and Kenya.

BIOLOGY. Unknown.

DISCUSSION. The original description of *O. miniatus* by Uvarov (1930*a*: 177) was based on a single female specimen collected at 2025 m in the Surud Range of N. Somalia. More recently specimens have been collected in southern Somalia and in Kenya which are much larger, with the hind wing fascia better developed. A close comparison with the holotype is no longer possible since it has been reduced by insect damage to a shell consisting of the pronotum, tegmina, hind wings and left mid leg. However, all the known specimens appear to belong to one species, though further collecting in northern Somalia may demonstrate that the population from which the holotype came is a montane relict which has diverged sufficiently from the main population of the species further south to be considered as a separate subspecies. The male of this species, previously unknown, is here described for the first time.

Oedaleus nadiae **sp. n.**

(Figs 30, 58, 138–141, 156)

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together. Flagellum 20-segmented. Fastigium of vertex longer than wide, subtriangular, concave, with well-defined margin; frons in profile slightly convex, almost straight; frontal ridge strongly narrowed just below fastigium and with a slight constriction just ventral to median ocellus. Eyes about one and a half times as deep as wide. Pronotum tectiform, strongly rugose, median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal X-marking placed on raised ridges; hind margin acutangular; mesosternal interspace anteriorly narrower than metasternal but wider posteriorly. Tegmen surpassing folded hind knees by one-tenth to one-third of hind femur length; tibia with 10 outer and 11–12 inner spines; inner apical spurs nearly twice as long as outer; apical tarsal segment twice claw length; arolium about half claw length. Cerci length twice basal width. Genitalia (Figs 138–140): cingular apodemes medium length, evenly tapering; rami short, apices of cingular and apical penis valves long and exposed, the latter with acute chisel-like apices and pronounced lobular subapical ventral process. Epiphallus trapezoidal with lateral plates indented; bridge flat and thick, lophi with inner and outer lobes subequal in size. Anterior projections large, rectangular, posterior projections rectangular.

General coloration mottled brown with light brown or green markings on frons, vertex, genae and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half. Broad pale pronotal X-marking (Fig. 58) sometimes continuous posteriorly with pale band fringing hind margin of pronotum. Tegmen infuscate brown in basal two-thirds with two pale transverse bands reaching to first anal vein posteriorly; apical third of tegmen clear, with dark speckles. Hind wing lacking fascia, with pale crimson basal area and darkened main veins. Outer surface of hind femora with three oblique dark bands separated by lighter areas; internal surface with dark brown medial area; interior ventral carina orange; hind knees blackish, tibiae orange.

♀. Antennae 22-segmented. Pronotum heavily rugose, warty. Ovipositor valves pale with weakly sclerotized excurved apices (Fig. 58). Spermatheca (Fig. 141) with apical diverticulum elongated, tapering, and with short finger-like subapical diverticulum.

MEASUREMENTS (all known specimens)

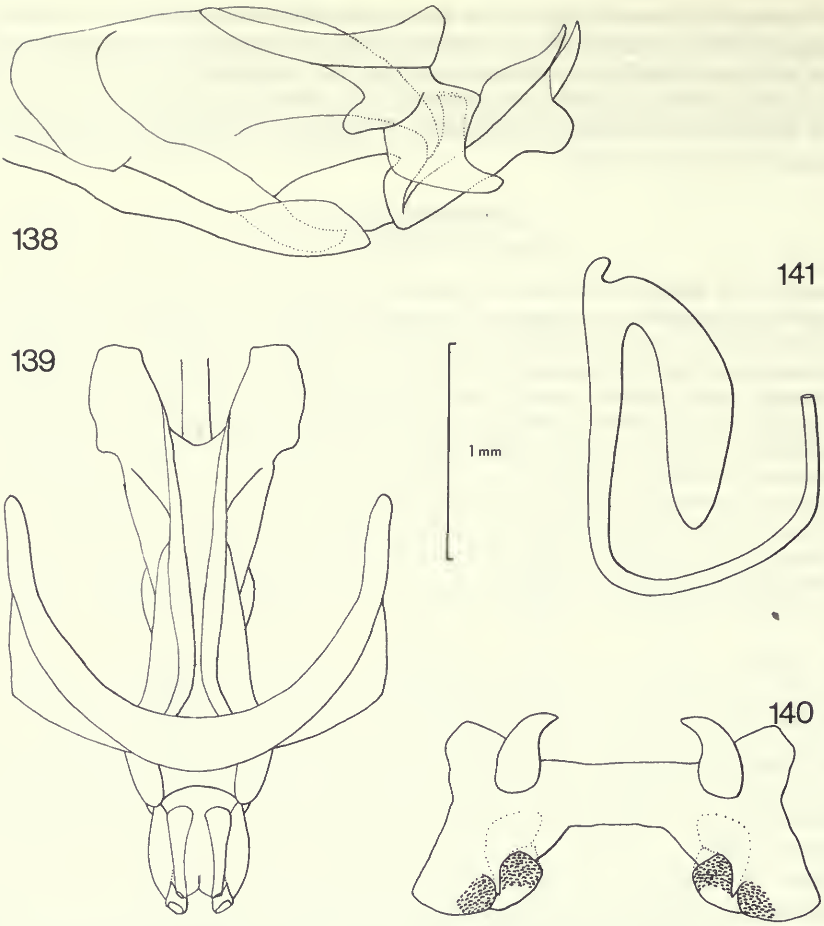
Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23·68	3·96	4·78	16·88	11·83	3·53	3·35	3·54
Range	21·6– 25·4	3·6– 4·2	4·3– 5·4	15·4– 18·5	10·6– 12·6	3·2– 3·9	3·3– 3·5	3·2– 4·0
S.D.	1·252	0·170	0·314	1·04	0·725	0·207	0·085	0·276
n	8	8	8	8	8	8	8	8

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31·96	6·05	7·18	22·05	15·41	4·53	3·41	3·10
Range	27·4– 36·5	5·4– 6·7	6·0– 8·6	18·5– 25·5	12·7– 17·9	3·7– 5·3	3·2– 4·0	2·8– 3·4
S.D.	2·835	0·472	0·840	2·067	1·556	0·547	0·173	0·161
n	16	17	17	16	17	17	17	16

AFFINITIES. *O. nadiae* is most closely allied to *O. miniatus*. Principal characters in common are the general shape (rather stocky in the female), red hind wing, short cingular rami with exposed



Figs 138–141 *O. nadiae,* genitalia. 138, endophallus and cingulum, lateral view; 139, same, dorsal view; 140, epiphallus; 141, spermatheca.

cingular and apical penis valves with very large subapical ventral processes (Fig. 138), and inner and outer lobes of epiphallic lophi small and nearly equal in size. The principal differences are that *O. nadiae* has an unbanded hind wing, a less elongated epiphallus, and the male subgenital plate not produced into a sharp point.

MATERIAL EXAMINED

Holotype ♂, **Somali Republic:** between Hargeisa and Mandera, 7.vi.1955 (*Uvarov*) (BMNH).

Paratypes. **Somali Republic:** between Hargeisa and Mandera, 7.vi.1955 (*Uvarov*); 1 ♀, El Rago, 8.xii.1953 (*Popov*); 4 ♀, Las Anod, 1935 (*Peck*); 2 ♂, 2 ♀, same data, 16.xi.1935; 1 ♂, 2 ♀, Ainabo, 8.vi.1952 (*Popov*); 2 ♀, 40 km WNW. of Borama, Aubube, 25.v.1958 (*Hussein*); 1 ♂, 17·7 km NW. of Borama, 7.vi.1957 (*Roffey*); 1 ♂, 1 ♀, Gardo plain, nr Hargeisa, 23.v.1967 (*Yussuf*); 2 ♂, N. region, between Mait and Las Khoreh, 20.v.1967 (*Yussuf*); 2 ♀, El Donfar, 10°40′N, 49°05′E, 22.v.1967 (*Yussuf*).

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). This species is known only from the northern region of Somalia.

BIOLOGY. Unknown.

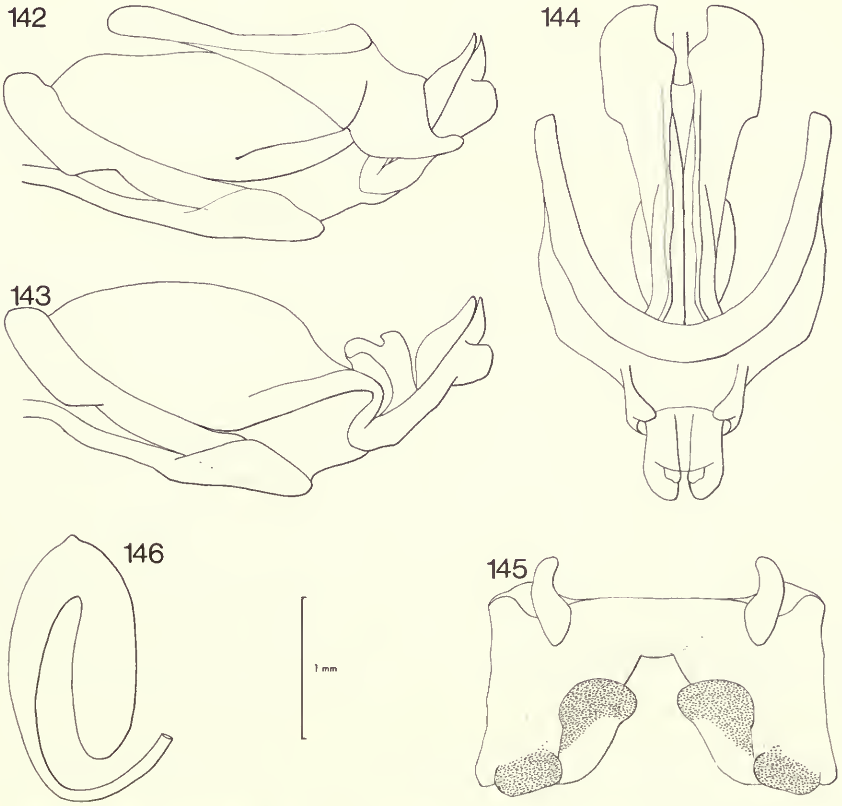
DISCUSSION. This species is named in honour of Dr Nadia Waloff.

Oedaleus inornatus Schulthess-Schindler, 1898
(Figs 25, 57, 142–146, 156)

Oedaleus inornatus Schulthess-Schindler, 1898: 27. Holotype ♀, SOMALI REPUBLIC: Dolo, viii.1893 (*E. Ruspoli*) (MCSN, Genoa).

REDESCRIPTION. ♂. Integument rugulose and pitted. Antennae one and one-third times as long as head and pronotum together, flagellum 22- to 23-segmented. Fastigium longer than wide, shallowly concave, narrowing to half maximum width anteriorly, margins only slightly raised; frons in profile slightly convex; frontal ridge slightly expanded above median ocellus. Eyes one and two-fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing folded hind knees by one-quarter to one-third of hind femur length. Hind tibia with 13 inner and 11–12 outer spines; inner apical spurs about one and one-third times as long as outer; apical tarsal segment nearly twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 142–145): cingular apodemes long and of moderate thickness and curvature; rami short, cingular and apical penis valves protruding strongly; subapical ventral process large; epiphallus rectangular, bridge thick, narrow, lophi very large and heavily sclerotized, inner lobes larger than outer; anterior and posterior projections lobate, acutely rounded.

General coloration brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora; green forms relatively rare. Tegmen infuscate brown in basal half with three variable transverse bars or blotches situated one-sixth, one-third, and one-half of distance along from base; apical half clear with variable brown patches. Hind wing without fascia but with infuscate wing tip, and occasionally, faint traces of fascia near hind margin; basal area pale yellow. Hind femur with three variable oblique dark bands on outer medial and upper marginal areas, basal pair of bands



Figs 142–146 *O. inornatus*, genitalia. 142, endophallus and cingulum, lateral view; 143, same, cingulum removed; 144, endophallus and cingulum, dorsal view; 145, epiphallus; 146, spermatheca.

elided on inner surface to form large black area; ventral surface scarlet; hind knees black, hind tibia with narrow dark basal ring and broad pale subbasal area, otherwise scarlet.

♀. Hind femora and tibiae less distinctly red than male. Ventral ovipositor valves (Fig. 57) elongate triangular, well sclerotized, with smoothly incurved exterior margins. Spermatheca (Fig. 146) with apical diverticulum vestigial.

MEASUREMENTS

Sample from Somali Republic: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	33·16	5·11	6·08	23·88	17·14	4·36	3·93	3·92
Range	27·4–37·3	4·4–5·7	5·2–6·8	19·5–27·0	15·1–19·3	3·5–4·9	3·7–4·1	3·6–4·2
S.D.	3·658	0·453	0·528	2·754	1·63	0·40	0·157	0·207
n	12	12	12	12	12	12	12	12
Females								
Mean	43·16	6·98	7·83	30·82	21·12	5·3	3·99	3·91
Range	33·6–48·9	6·2–7·9	6·4–9·3	23·6–35·2	16·7–25·3	4·3–6·1	3·8–4·4	3·5–4·5
S.D.	4·57	0·556	0·766	3·357	2·155	0·508	0·156	0·271
n	18	19	19	18	19	19	19	18

AFFINITIES. *inornatus* is characterized by the total absence of a wing band and by the very robust genitalia, in particular the epiphallus with its very large lophi. It is impossible to relate this species to the others with any degree of certainty. It may possibly be an offshoot of the *senegalensis*-group.

MATERIAL EXAMINED

Somali Republic: 2 ♂, 4 ♀, northern region, between Mait and Las Khoreh, 20.v.1967 (Yussuf); 2 ♂, Gardo plain, nr Hargeisa, 23.v.1967 (*Yussuf*); 4 ♂, 4 ♀, Haded plain, 24.v.1967 (*Yussuf*); 1 ♂, Burao area, 27.v.1967 (*Yussuf*); 1 ♂, Las Khoreh, 21.v.1967 (*Yussuf*); 1 ♂, 08°15′N, 47°50′E, 24.xi.1946 (*Wood*); 3 ♀, El Donfar, 10°40′N, 49°05′E, 22.v.1967 (*Yussuf*); 1 ♀, Las Anod, 1935 (*Peck*); 1 ♂, 1 ♀, same data, xi.1935; 1 ♀, same data, 8.i.1936; 2 ♂, same data, 16.xi.1935; 1 ♀, Derkengenyu, 21.xi.1935 (*Peck*); 1 ♀, Bul Beali, 08°15′N, 47°50′E, 24.xi.1946 (*Wood*); 2 ♀, Dan Gudban hills, 08°15′N, 47°15′E, 24.xi.1947 (*Wood*); 1 ♀, Borama, 1500 m, 13.vi.1952 (*Popov*). **Ethiopia:** 4 ♂, 2 ♀, Mega, Borama, x.1951 (*Bellehu*); 1 ♀, Harerge pr., Melka Werer, Inst. Agr. Res., 14·5 km ENE. of station, grassland pasture, 30.ix.1975 (*Jago*) (MA, Addis Ababa). **Kenya:** 6 ♂, 9 ♀, on Emali – Chyulu Hills road, 6 km E. of Makutano, flat plain, grass with *Acacia* trees, 02°31′S, 37°34·5′E, 1050 m, 1972 (*Robertson*); 2 ♂, Emali – Makutano – Chyulu Hills road, 16 km E. of Makutano, roadside, short open grass plains just W. of Elmau Hill, c. 1100 m, 02°31′S, 37°40′E, 1972 (*Robertson*); 1 ♀, Lesai area, 29 km SE. of Korondil, Moyale dist., 02°55′N, 39°15′E, thorn bush, 15.vi.1946 (*Kevan*); 1 ♀, Chopa Gof, Marsabit, 02°25′N, 38°03′E, grass and scrubby bushes, 13.vi.1946 (*Kevan*); same data, 29.ii.1944; 1 ♀, Wajir dist., Well Marer, 02°05′N, 40°30′E, desert grass and thorn bush, 21.vi.1944 (*Kevan*); 1 ♀, N.F.D., El Wak, desert grass, thorn bush, 5.xii.1944 (*Kevan*); 1 ♀, same data, 25.v.1944; 1 ♂, 4 ♀, 17 km N. of Loglogu, at side of main road, 02°09′N, 37°53′E, 900 m, 19.v.1975 (*Robertson*) (COPR, London); 1 ♂, nr Ferguson's Gulf, L. Turkana, hillside nr hill called Luola, 03°24′N, 35°49′E, 16 km along new road to Lodwar, 540 m, 4.vii.1975 (*Robertson*) (COPR, London); 1 ♀, Ferguson's Gulf, L. Turkana, Angling Lodge, 03°33′N, 35°56′E, 370 m, 3.v.1975 (*Robertson*) (COPR, London).

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). Widely distributed but not common throughout the drier areas of north-eastern Africa.

BIOLOGY. Unknown. A gynandromorph specimen of this species has been described (Ritchie, 1978*b*).

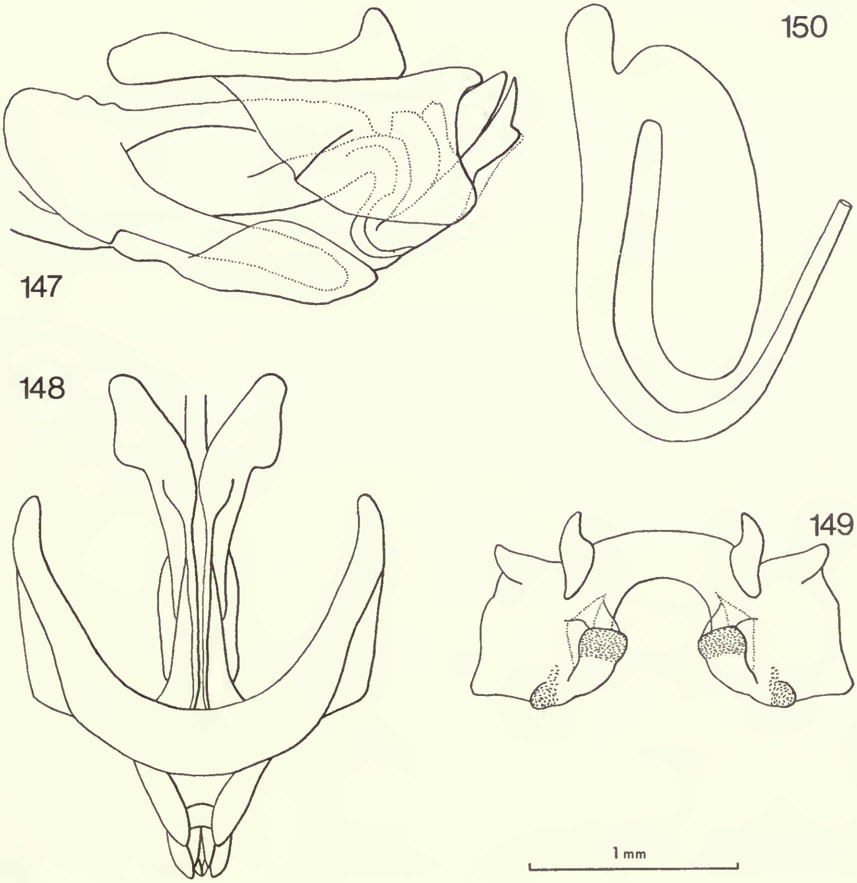
Oedaleus flavus (Linnaeus, 1758)
(Figs 17, 34, 49, 50, 147–150, 155)

Gryllus Locusta flavus Linnaeus, 1758: 433.

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugose and warty. Antennae slightly longer than head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, widest medially, tapering both anteriorly and posteriorly, concave, with well-defined margins; frons in profile convex; frontal ridge almost parallel-sided, slightly divergent between antennal bases. Eyes about one and two-fifths times as long as wide. Pronotum tectiform with sparse warts, at least in prozona; median carina arcuate, intersected by posterior sulcus; hind margin of pronotum acutangular. Tegmen surpassing folded hind knees by about one-fifth to one-third of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment one and four-fifths length of claw; arolium less than half claw length. Cerci two and a half times as long as basal width. Genitalia (Figs 147–149): cingular apodemes medium length, medially thickened; rami slender, elongate, cingular valves and apical penis valves short; subapical ventral process small; epiphallus trapezoidal, lateral plates slightly excurved; bridge arched, thick; lophi with inner lobes larger than outer; anterior projections small, acutely rounded; posterior projections rectangular, rounded.

General coloration dark brown, with lighter brown (or rarely green) markings on frons, vertex, genae, and



Figs 147–150 *O. flavus,* genitalia. 147, endophallus and cingulum, lateral view; 148, same, dorsal view; 149, epiphallus; 150, spermatheca.

pronotum. Tegmen infuscate brown in basal two-thirds with three pale transverse bars at intervals of one-quarter, one-half, and two-thirds along from base; apical third clear with brown speckles. Hind wing fascia (Fig. 17) complete, continued half way towards apex of wing between first radial vein and radial sector; wing tip variably infuscate; basal area of wing bright opaque lemon-yellow. Outer surface of hind femora with three oblique dark bands; hind knees blackish, hind tibiae orange-red.

♀. Dorsal surface of pronotum with large warts and posterior arms of X-marking very thick (Fig. 34). Hind wing tip not clouded. Ovipositor valves strongly sclerotized and excurved. Spermatheca (Fig. 150) with apical diverticulum bulbous, preapical diverticulum stout.

AFFINITIES. *O. flavus* is probably allied to *O. instillatus* on the basis of its epiphallus having small lophi (Fig. 149) and the same characteristic suggests a link with *O. plenus* with which it may be confused on superficial examination. The bright yellow basal area of the hind wing is, however, a sufficient diagnostic character.

DISTRIBUTION (Fig. 155, and Biogeography section, p. 157). Widely distributed in eastern and southern Africa with a broad discontinuity corresponding with the *Brachystegia* woodland zone.

BIOLOGY. Little is known of the biology of this species. It was reported by Ballard (1914) as a pest of tobacco in Malawi. Phipps (1959) recorded mean numbers of 35·0 and 36·8 ovarioles per female in two samples of two and four specimens respectively in Tanzania. The chromosomes have been briefly discussed by Nolte (1939).

The two subspecies of *O. flavus* may be separated by the following keys.

Males

1 Interior surface of hind femur with one transverse and one U-shaped dark band, not intersecting the internal ventro-lateral carina; basal half of interior surface, internal ventro-lateral carina, and ventral surface suffused with red (East Africa) . . . ***O. flavus somaliensis*** (Sjöstedt) (p. 152)

– Interior surface of hind femur with dark bands enlarged and crossing internal ventro-lateral carina onto ventral surface; central portion of interior surface suffused with mauve or black, never red (South Africa) . . . . ***O. flavus flavus*** (Linnaeus) (p. 150)

Females

1 Ventral surface of hind femur, particularly internal ventro-lateral carina, suffused with red, sometimes discoloured, never black; basivalvular sclerite of ventral ovipositor valves smooth (Fig. 50) . . . . ***O. flavus somaliensis*** (Sjöstedt) (p. 152)

– Ventral surface of hind femur, particularly in inner half, suffused with black, never red; basivalvular sclerite of ventral ovipositor valves with raised warts in posterior half (Fig. 49) ***O. flavus flavus*** (Linnaeus) (p. 150)

Oedaleus flavus flavus (Linnaeus, 1758)

Gryllus Locusta flavus Linnaeus, 1758: 433. Lectotype ♀, AFRICA (ZIUU, Uppsala), designated by Dirsh (1961: 317) [*not* in LS, London, as stated by Dirsh, *op. cit.*] [examined].

Gryllus flavus (Linnaeus) Fabricius, 1775: 292 [locality: Piedmont, indicates partial confusion with *Oedaleus decorus* (Germar)].

Acrydium flavum (Linnaeus) Olivier, 1791: 227. [Incorrectly gives *Acrydium nigrofasciatum* Degeer, 1773 as synonym.]

Gryllus flavus (Linnaeus) Petagna, 1792: 319. [Incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym.]

Oedipoda flava (Linnaeus) Serville, 1831: 288.

Oedipoda flava (Linnaeus); Burmeister, 1838: 643. [Incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym.]

Pachytylus (*Oedaleus*) *flavus* (Linnaeus) Stål, 1873: 125.

Humbella flava (Linnaeus) Saussure, 1884: 107.

Oedaleus nigrofasciatus var. *citrinus* Saussure, 1888: 41. LECTOTYPE ♂, SOUTH AFRICA: 'Cap.' (MHN, Geneva), here designated [examined]. [Synonymized by Dirsh, 1961*a*: 317.]

Oedalus (sic) *citrinus* (Saussure); Distant, 1892: 260.

Oedaleus citrinus (Saussure); Kirby, 1910: 225.

Oedaleus flavus (Linnaeus) Kirby, 1902*a*: 73. [Incorrectly gives *Oedaleus nigrofasciatus* Degeer as synonym.]

Humbe flava (Linnaeus) Kirby, 1910: 215.

Oedaleus flavus (Linnaeus); Dirsh, 1961*a*: 317. [Reinstates original usage.]

MEASUREMENTS

Sample from South Africa: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28·19	4·27	5·45	20·99	13·92	3·71	3·75	3·85
Range	26·4– 29·9	3·9– 4·7	5·1– 5·9	19·6– 22·4	12·9– 15·2	3·3– 4·2	3·6– 4·0	3·7– 4·0
S.D.	1·212	0·206	0·228	1·041	0·762	0·264	0·126	0·093
n	11	11	11	11	11	11	11	11

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	37·0	5·79	7·04	27·58	17·78	4·93	3·61	3·93
Range	34·8– 39·9	5·0– 6·3	6·3– 7·8	26·0– 29·5	16·1– 19·4	4·3– 5·2	3·4– 3·8	3·7– 4·3
S.D.	1·537	0·346	0·402	1·015	0·844	0·277	0·114	0·165
n	11	11	11	11	11	11	11	11

MATERIAL EXAMINED

Gryllus Locusta flavus Linnaeus, lectotype ♀, **Africa:** no further data (ZIUU, Uppsala). *Oedaleus nigrofasciatus* var. *citrinus* Saussure, lectotype ♂, **South Africa:** Cape of Good Hope, no further data (MHN, Geneva).

In addition to the lectotypes, 94 specimens were examined from the following localities. **Angola:** Tundavala, 13–16 km NW. of Sa da Bandeira, 14°50'S, 13°25'E, 1800–2100 m. **Zimbabwe:** Gwanda, 900 m; Odzi distr., Zimbabwe, 1050–1440 m; Matopo Hills; Shangani, De Beers ranch; nr Salisbury, Bindura. **Mozambique:** Malongotiba; Namaacha; Matola Rio; Umbeluzi; Inolabane. **Namibia:** Oshikango, 1100 m; 21 km NW. of Oshakati, Ovamboland; Otjangasema, Kaokoveld N. **Botswana:** 4·8 km NE. of Maun; Bathoon dam, Kanye; Mogobane; Metsimaklaba. **South Africa:** Transvaal, Louis Trichardt; T., Zoutpansberg; T., Pretoria; T., N. of Nelspruit; T., Tom Burke, 23°04'S, 28°00'E; T., R Limpopo, 23°00'S, 27°57'E; T., Kruger National Park, 16 km NE. of Skukuza; T., Klaserie Nature area, Klaserie R; T., 28 km E. of Barberton, 510 m; T., Barberton; Natal, 16 km N. of Ubombo, 160 m; 4·8 km N. of Ubombo, 300 m; N., Pietermaritzburg; N., Zululand, Lower Umfolosi R.; N., Durban; N., Klipfontein; Cape Province, 35·4 km W. of Cofimvaba, 940 m; C.P., 13 km S. of Balfour, 500 m; C.P., Grahamstown; C.P., Katberg, 1200 m; C.P., Fish R. valley; C.P., 32 km ENE. of Bredasdorp, Kars (Salt) R.; C.P., 32 km SE. of Swellendam; C.P., Zuurberg Pass, 24 km N. of Addo; C.P., Oakhill, 48 km NE. of Port Elizabeth; C.P., Capetown; C.P., De Hoop Vlei, 32 km E. of Bredasdorp; C.P., Cape of Good Hope; C.P., Resolution, Ft Brown.

DISCUSSION. The male specimen of *O. nigrofasciatus* var. *citrinus* here designated as lectotype bears a label in Saussure's hand: '*citrinus* Sss. ♀ [incorrect sex] Cap. Type'. The status of six female specimens in the collection is unclear and they have accordingly not been designated as paralectotypes.

Oedaleus flavus somaliensis (Sjöstedt, 1931) **comb. et stat. n.**

Gastrimargus somaliensis Sjöstedt, 1931*b*: 26. Holotype ♀, SOMALI REPUBLIC (NR, Stockholm) [examined].

MEASUREMENTS
Sample from Kenya: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27·4	4·11	5·12	20·56	13·45	3·59	3·74	4·03
Range	24·7–	3·7–	4·5–	18·5–	11·6–	3·3–	3·4–	3·6–
	29·3	4·5	5·6	22·2	15·1	4·0	4·0	4·5
S.D.	1·216	0·217	0·303	1·004	0·865	0·183	0·136	0·231
n	22	22	22	22	22	22	22	22

Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38·74	6·18	7·1	29·08	18·49	5·11	3·62	4·10
Range	33·3–	5·5–	6·1–	24·7–	15·7–	4·5–	3·4–	3·8–
	45·6	6·5	7·8	34·4	21·6	5·7	3·8	4·5
S.D.	2·752	0·385	0·472	2·147	1·294	0·324	0·130	0·208
n	14	14	13	14	14	14	14	13

MATERIAL EXAMINED

Gastrimargus somaliensis Sjöstedt, holotype ♀, **Somali Republic:** Alessandra, Chismaio, 1928 (*Kinell*) (NR, Stockholm).

In addition to the holotype, 88 specimens were examined from the following localities. **Somali Republic:** nr Afmadu; Iscia Baidoa; S. Region, 11·3 km N. of Bulo Burti; Mogadiscio. **Kenya:** Hola (Galole), 01°30′S, 40°00′E, 70 m; Tana R. Distr., Hola (Galole, 01°25′S, 39°57′E, less than 100 m, 20 km N. of Hola on Garsen to Garissa road; 30 km S. of Hola on Garsen to Malindi road, 01°47′S, 40°02′E, 45 m; 85 km N. of Malindi, on Malindi to Garsen road, 02°28′S, 40°08′E, 30 m; 80 km W. of Malindi, on Malindi – Sala – Tsavo road, 03°06′S, 39°22′E, 150 km; N. F. D., Moyale; Ngong; Ngong forest; Athi Plains; Garsen; Turkana, Kacheliba; Mida Creek, Kilifi distr., 03°19′S, 39°58′E, sea level; approx. 3 km E. of Taru village, 03°45·5′S, 39°10′E, 330 m; Lukenia Hill, 35 km from Nairobi, on Mombasa road, site about 3·2 km along side road, 01°29′S, 37°04′E, 1740 m. **Uganda:** Moroto; Kidepo National Park, Kidepo valley, approx. 03°55′N, 33°50′E; Karamoja. **Sudan:** Mongalla; Juba, Mongalla. **Tanzania:** Morogoro distr., Mikumi; Kilosa; Rukwa Rift, Moomba R.; Usasi, clearings, 72·5 km NW. of Singida; Old Shinyanga; Samui, nr Manyon R., S. of Shinyanga; Tinde; 32 km SW. of Shinyanga; Tindiga; Mikumi; Mlingano, Ngomeni.

DISCUSSION. *Gastrimargus somaliensis* Sjöstedt (1931*b*) is here considered as a subspecies or geographical race of *O. flavus*. The external morphology and male genitalia of the two forms are identical apart from the minor differences detailed in the key above (p. 150). Despite these consistent differences the overall shape and size of the animals has remained remarkably constant in the two disjunct populations. Tegmen length is slightly significantly ($P < 0·05$) larger in East African females than in South African, but in males there is no significant difference. Pronotum length is significantly smaller ($P < 0·002$) in East African males than South African, but in females there is no significant difference. The TL/PL ratio is significantly higher in East African specimens ($P < 0·01$ ♂, $< 0·05$ ♀) and the sexual dimorphism as measured by mean T♀/T♂ (Farrow, 1972) is greater in the former (1·414) than the latter (1·314).

The present interrupted distribution of the two races probably resulted from the recent interposition of the *Brachystegia* woodland across a previously continuous range of savannah (Van Zinderen Bakker, 1976). As described above (p. 156) *O. plenus plenus* also has two populations separated by the woodland, but without having undergone any apparent morphological divergence. For this reason and in view of the small amount of divergence which can be observed in the two populations of *O. flavus*, the process of speciation is considered to be incomplete.

Biogeography of the genus *Oedaleus*

Relationships within the genus

The genus *Oedaleus* comprises a homogeneous group of oedipodine grasshoppers colonizing a wide range of grassland habitats throughout the tropical and warmer temperate regions of the Old World. Before any analysis of the influences that have shaped the present distribution of the genus can be attempted it is necessary to describe the groupings of species which can be made on morphological gounds. These are tabulated below.

Group I
O. senegalensis
O. nigrofasciatus
O. australis
O. abruptus
O. virgula
O. johnstoni
O. nigeriensis
O. carvalhoi
O. plenus
O. decorus
O. infernalis
O. formosanus
O. interruptus

Group II
O. instillatus
O. obtusangulus
O. rosescens

Group III
O. miniatus
O. nadiae

Ungrouped species
O. inornatus
O. flavus

Group I are linked by the possession of the following combination of characters: 1, similar genitalia having epiphallic lophi with unequal sized lobes; 2, the basal area of the hind wing pale yellow; 3, smooth integument with pronounced green-brown polymorphism. *O. interruptus* is unusual in having a strongly acutangular hind margin to the pronotum, but is otherwise a member of this group. Group II have the epiphallus almost square with small, equal sized lobes to the lophi. Group III have pink wings and rugose integument and are probably closely related although each species has peculiarities which suggest that they have been genetically isolated one from the other over a long period. *O. rosescens,* another species with pink wings, is placed in group II since it resembles the other two species of that group in all other characters.

Geographical origin of the genus

Analysis of the existing distribution of the genus strongly suggests an origin within the Ethiopian Region. The evidence for this can be summarized as follows.

1. The species endemic to Africa show the greatest range of interspecific morphological diversity, whereas those outside Africa can be placed in one or other of the African groups of species.
2. More than half of the known species (13) are found in Africa south of the Sahara. One other is known from North Africa and yet another species is endemic to Madagascar.
3. The genera most closely related to *Oedaleus* are either endemic to the Ethiopian Region (e.g. *Humbe* Bolívar, *Oreacris* Bolívar, *Locustana* Uvarov), or are Malagasian (e.g. *Pycnocrania* Uvarov), or are at least well represented in Africa (e.g. *Locusta* Linnaeus, *Gastrimargus*).

La Greca (1970) has drawn attention to the danger of assuming an Ethiopian origin for groups which may have entered Africa from southern Europe or western Asia, and whose present distribution may represent a relic of a much more extensive fossil or prehistoric range which would have included those areas. He cites the examples of the lion and the rhinoceros whose present limited distribution has been reduced largely by human activity. As to the savannah grasshoppers, however, it seems improbable that anything short of major habitat degradation would have brought about multiple extinctions. In Australia some flightless members of the endemic subfamily Morabinae are reported to survive only in graveyards and other refuges where sheep grazing is prevented (Key, 1974). However, *Oedaleus* together with several other Oedipodines is able to survive under a wide range of ecological conditions, largely because of its effective egg diapause and the high mobility of the adults. For these reasons an African origin, or at least a primary radiation within Africa, seems most probable. To gain some idea of the forces which could have brought about the present day radiation of species it is necessary to examine some of the major features, past and present, of the African biomes.

The Pleistocene in Africa

Moreau (1966), in his study of the bird faunas of Africa, has reviewed the climatic changes of the Pleistocene in Africa, and has presented strong circumstantial evidence for his belief that the forces that have shaped the avian fauna have, for the most part, operated within the last 70 000 years. At present there is no coherent chronological scheme that would harmonize all the known geological changes which have occurred in different parts of Africa within that period of time. However, it is possible to date some Pleistocene features in Africa and to relate them to events both in different parts of Africa itself and in Europe.

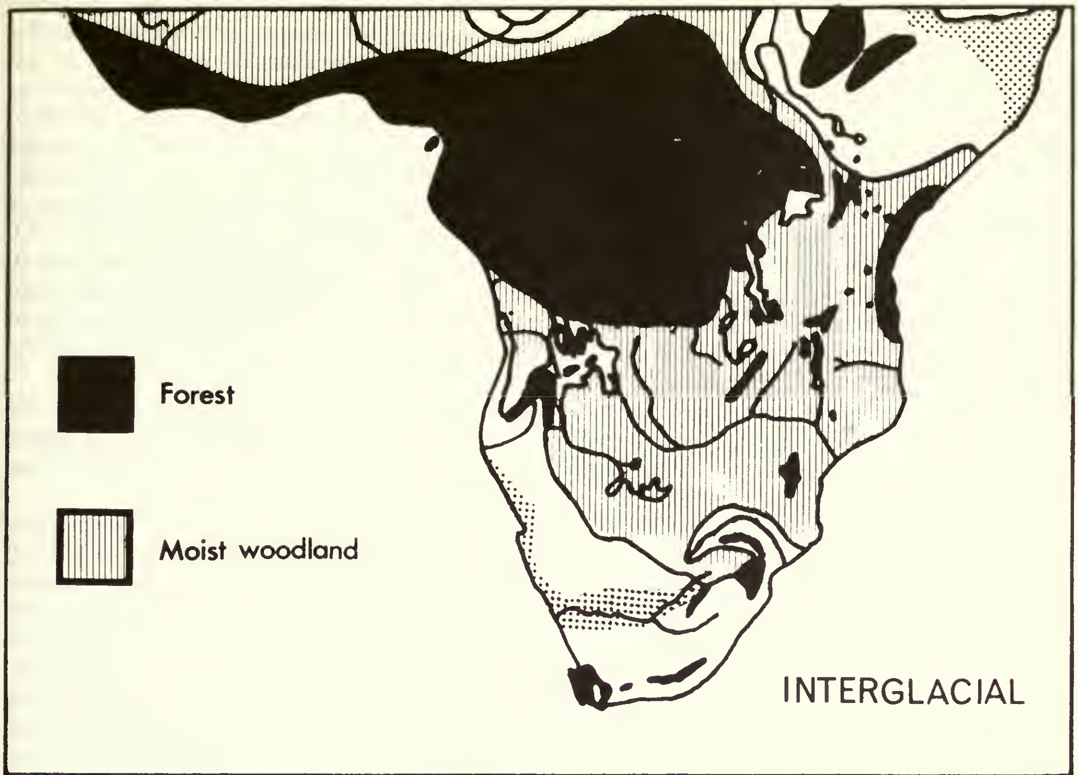
The two major influences on vegetation in the past have been changes in temperature and humidity and the most significant fluctuations in both have been associated with glaciation. As well as a direct lowering of temperature, glaciation has a complex effect on atmospheric circulation which in turn causes changes in the rainfall pattern which are the subject of opposed theories. In the last one million years there have been four glaciations, each with a similar temperature minimum and each separated by an interglacial period with higher peak temperatures than at present. The course of the last glaciation is better known than that of the previous ones and serves as a model in considering some of the dramatic changes which have repeatedly affected both the climate and vegetation of Africa. There is, however, the important reservation that human influence has been much more significant since the last glaciation than at any earlier period.

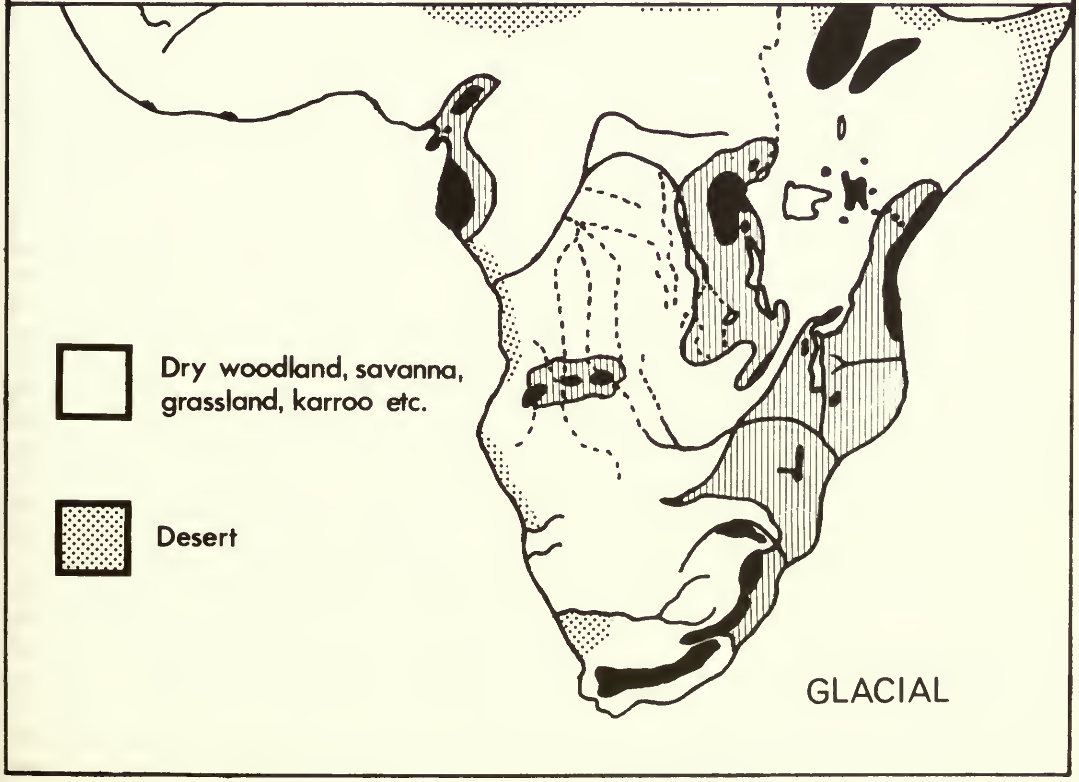
The last glaciation began around 70 000 years B.P. (before present), and its last severe stage lasted from 25 000–15 000 B.P. with a peak at 19 000 correlated with arctic conditions in central Europe. From around 16 000 B.P. the temperature rose very sharply except for brief cold relapses around 10 500 B.P. and again between 5500 and 4700 B.P. (Van Zinderen Bakker, 1969*a*). Present temperatures were reached around 8000 B.P., then exceeded by as much as 2°C around 6000 B.P. Finally, between 1400 and 1850 AD temperatures were slightly lower than now (Moreau, 1966). These cyclical temperature changes, which are presumed to be of cosmic origin, have exercised a profound effect on plant and animal distribution patterns both directly and through their influence on precipitation, evaporation and ocean currents. The results of this influence are discussed below on a regional basis in relation to the distribution of the species of the genus *Oedaleus*.

The southern African *Oedaleus* fauna

According to Moreau (1966), the most stable parts of Africa during the Pleistocene have been the Namib and Kalahari deserts of southern Africa and the Somali peninsula of eastern Africa. Van Zinderen Bakker (1975) has reviewed evidence relating to the age, origins and movements of the Namib and Kalahari and concludes that they originated in the Oligocene about 40–45 million years B.P. At glacial maxima these deserts have enlarged and moved northwards in response to the growth of the polar ice-cap and the attendant shift towards the equator of the climatic belts and cold upwelling at the convergence of the Benguela and Angola currents on the west coast of southern Africa. Other effects of glaciation would have included decreased precipitation from colder oceanic water and an increase in the incidence of violent winds (Van Zinderen Bakker, 1976), both of which would have an aridifying influence. Successive enlargements of the Kalahari have pushed the *Brachystegia* woodland and the lowland forest zones back towards the equator, at the same time dissecting them into a number of separate refuges. Van Zinderen Bakker (1976) has produced tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum showing how open savannah and dry grassland would have increased in extent, offering contact between eastern and southern Africa for the semi-arid biota including *Oedaleus* (Fig. 151). Conditions at the height of the last glaciation would have provided an

Fig. 151 Tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum (simplified from Van Zinderen Bakker, 1976).


Forest
Moist woodland
INTERGLACIAL


Dry woodland, savanna, grassland, karroo etc.
Desert
GLACIAL

opportunity, perhaps the most recent of several, for species of the east African savannah and semi-arid zones to mix with those occupying similar habitats south of the equator, and vice versa, in the temporary absence of the woodland barrier which is at present more than 500 miles wide. At the same time much of South Africa and Botswana would have deteriorated from *Acacia* grassland to desert or near desert. The montane grassland of southern Transvaal, Orange Free State, Lesotho, and south-east Cape Province would have descended as much as 1000 metres but would apparently have suffered no reduction in area and may have constituted a relatively stable habitat during the Pleistocene. Certainly *O. interruptus*, the most distinct of the southern African species, is restricted to this habitat (Fig. 152) though apparently not found above about 2500 m. *O. nigrofasciatus*, another southern species, also favours the montane grassland (Fig. 152), whereas *O. carvalhoi* does not occur there (Fig. 152) although both species are found together further north and west across the *Acacia* and 'Mopane' wooded savannah. Both species bear a marked similarity to species found to the north of the *Brachystegia* belt. *O. nigrofasciatus* is morphologically almost indistinguishable from *O. senegalensis*, while *O. carvalhoi* shows a strong resemblance to *O. nigeriensis*. It is probable that these and other southern species and subspecies have been able to evolve in isolation from northern populations because of the periodic fragmentation of the humid woodland barrier described above. The importance of this barrier in the development of the African biota and the evidence in favour of it are discussed below (p. 171).

The two subspecies of *O. plenus*, a southern African species (Fig. 153), have a geographically and ecologically wide distribution within the different vegetation types mapped by Keay (1959). The most widely distributed subspecies, *O. plenus plenus*, is found in NE. Tanzania in open *Acacia* savannah with a grass cover dominated by *Themeda triandra* (Rattray, 1960). To the south, the *Brachystegia* woodland belt and rift valley separate this population from the main population of the subspecies which forms a continuous belt across the drier 'Mopane' wooded savannah from SW. Angola to Mozambique and the steppe country of Botswana with a grass cover dominated by *Eragrostis*. Evidently the openness of the vegetation and the rainfall regime are of greater importance in delimiting the range of this subspecies than is the species composition of the

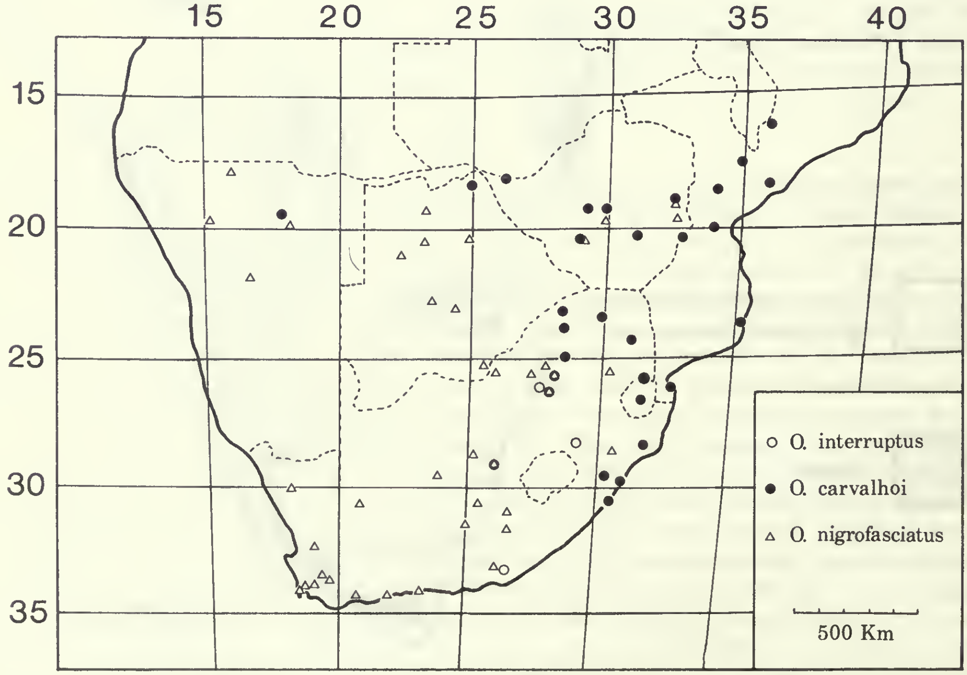


Fig. 152 Distribution of *Oedaleus* species in southern Africa.

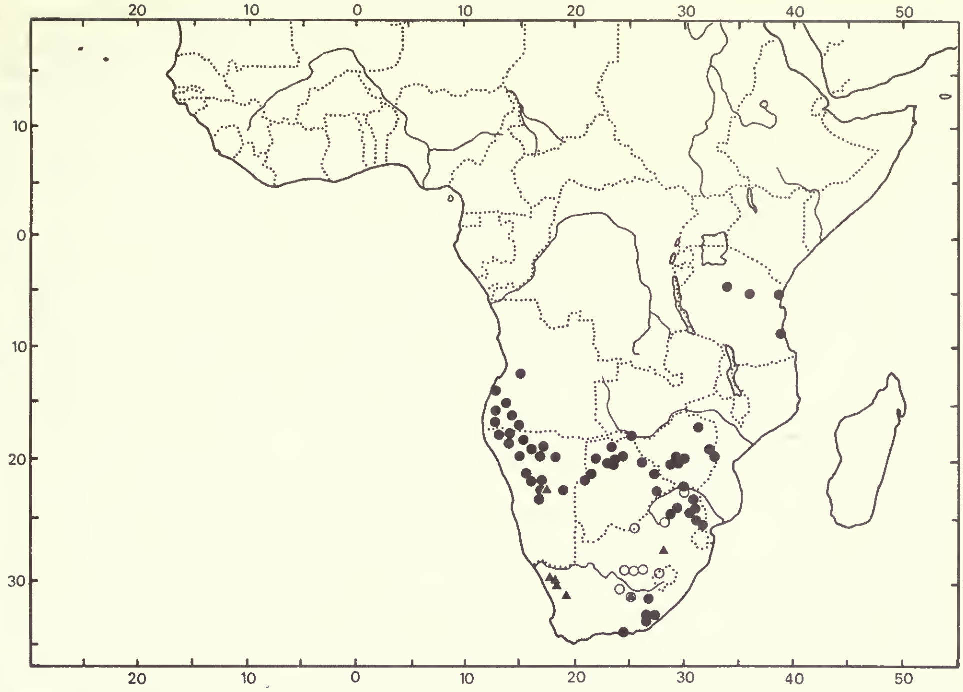


Fig. 153 Distribution of subspecies of *Oedaleus plenus* in southern Africa. Closed triangles, *O. p. plenus,* thin-lined form; closed circles, *O. p. plenus,* thick-lined form; open circles, *O. p. browni.*

grasslands which is quite different in the northern and southern savannahs. Further south there are two distinct populations. One of these, *O. plenus browni,* distinguished by the partial or total absence of the hind wing fascia, is apparently almost restricted to the montane grassland areas dominated by *Themeda* species, which are also the habitat of *O. interruptus,* although it does penetrate into areas dominated by *Hyparrhenia* species to the north and by *Eragrostis* species to the west on lower ground. Rattray (1960) quotes the view of an earlier worker, Acocks, who considered that these areas were also originally dominated by *Themeda* species which have been selectively removed by overgrazing. The montane habitat of this subspecies is entirely contained within that of *O. plenus plenus* which reaches the south coast around Port Elizabeth. Further west, in southern Cape Province an isolated population of *O. plenus plenus* has become adapted to the very distinct winter rainfall area of the western Karroo of Namaqualand. The seasonality of rainfall distribution in South Africa is shown in Fig. 154 (after Adamson, 1938). The figures represent the percentage of the total rainfall falling in the southern summer (October to March). The unusual climate of the region supports a complex plant community with many succulents and a large proportion of endemic genera, including the dominant grass *Ehrarta calycina.* It is probable that the tendency of specimens from this population to have finer pronotal markings is indicative of evolutionary divergence resulting from relative geographical isolation and partial asynchrony of the breeding season caused by the rainfall regime.

O. flavus, like *O. plenus,* occurs to north and south of the *Brachystegia* belt (Fig. 155), but the northern population extends northwards across the Equator into Kenya and Somalia whereas *O. plenus* apparently does not. Also unlike *O. plenus, O. flavus* occurs as one subspecies, *somaliensis,* in the northern *Acacia* savannah zone, and as another subspecies, *flavus,* in the south where it occupies a habitat similar to that of *O. nigrofasciatus,* even penetrating into the Macchia vegetation of the southern Cape. Evidently this is yet another example of colonization across the 'Miombo' woodland during a dry period, with subsequent isolation and divergence. The direction of the migration is assumed to be north to south in view of the greater richness of the *Oedaleus* fauna of

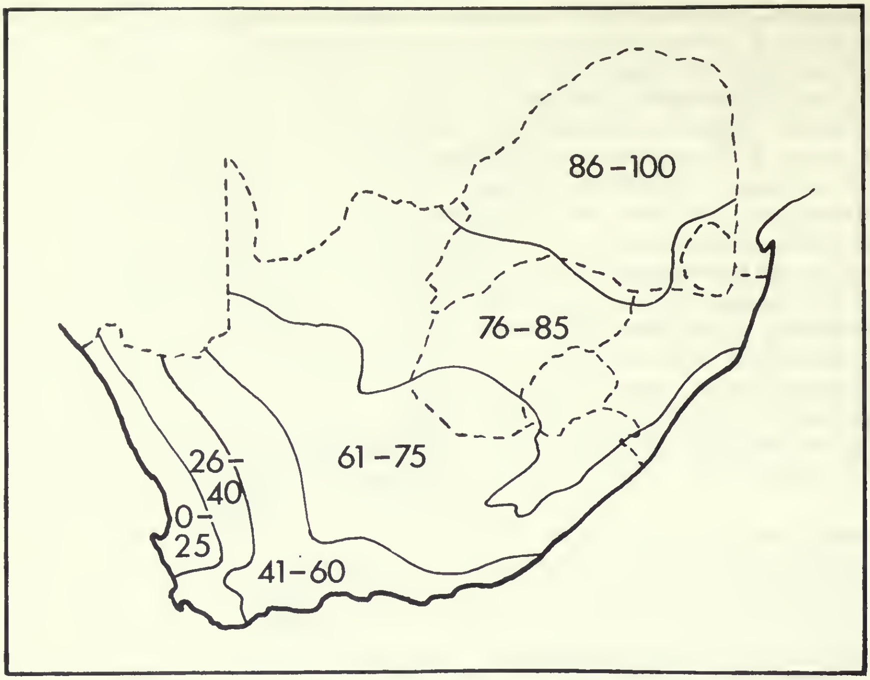

86–100
76–85
61–75
26–40
0–25
41–60

Fig. 154 Map of South Africa showing the percentage of total precipitation falling during the southern summer (October–March) (after Adamson, 1938).

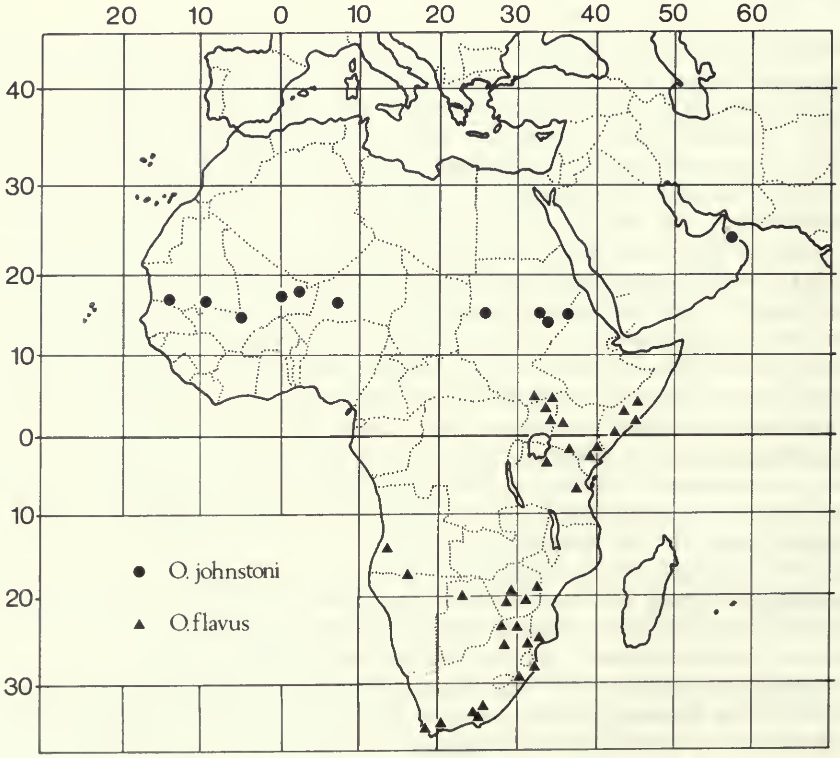

20
10
0
10
20
30
40
50
60
40
30
20
10
0
10
20
30
● O. johnstoni
▲ O. flavus

Fig. 155 Distribution of *Oedaleus* species in Africa.

East Africa. The simplest model is that of an East African focus with emigrants travelling south into an area where intrageneric competition would initially be less intense since fewer niches would be filled. However, it is possible that in some instances movement could have occurred in the reverse direction.

The *Oedaleus* fauna of the Somali peninsula

The most remarkable zone of speciation in *Oedaleus* has been the Somali peninsula. The arid horn of Africa is effectively separated from the latitudinal vegetation belts to the west by the Ethiopian highlands and Lake Turkana. Moreau (1966) lists the area as having more endemic birds than any other lowland non-forest zone in Africa. However, Winterbottom (1967) asserts that the South West Arid District has in fact much the larger avifauna, although direct comparison is impossible. Chapin (1923) considered the area as a distinct avifaunal district (the Somali Arid District) and Popov (1959) found this division relevant to the distribution of the aberrant endemic grasshopper genus *Sauracris* Burr. Both in *Sauracris* and *Oedaleus* it is noticeable that the maximum concentration of species occurs in the northern rangelands. This may in part be due to the wide diversity of structure, vegetation, and rainfall which are experienced within a relatively small area. The climatic zones of the Somali peninsula are shown in Fig. 156 (Griffiths, 1972). Zone I, the northern coastal strip, is characterized by winter rains and summer drought, though high humidity is maintained by land-sea breeze circulation. Zone II, further west, is little studied in terms of its acridid fauna. It is a summer rainfall area, barely reached by the Intertropical Convergence Zone at its most northerly extension, and very hot and arid. Zone III, south of Zones I and II, which constitutes the main portion of the northern rangelands, has a double rainfall peak in spring and autumn but there is great variability both between stations and from year to year (50–750 mm/yr). In this zone the lowest temperatures are reached in winter (December, January). Hemming (1966) and others have drawn attention to the degradation of this area by overgrazing in recent years. Despite this, however, Griffiths (1972) rejects the theory that the overall rainfall has declined during the last century. Further south, Zone IV, covering SE. Somalia and the SE. border of Ethiopia and NE. Kenya, also has a double peaked rainfall but experiences lowest temperatures in summer (July–August). Zone V consists of a SE. coastal strip with high rainfall affected by the Indian monsoon.

O. nadiae is restricted to Zone III, but its known distribution when superimposed on Hemming's Vegetation Map of Somalia (1966) does not suggest any strong havitat preference except for an apparent avoidance of the montane *Juniperus* forest, as would be expected. The floristic diversity of the six localities from which this species is recorded suggests that the major limitation of its range may be a preference for a winter temperature minimum rather than a summer one.

In all, four species of *Oedaleus* are endemic to the Somali peninsula, including *O. inornatus* (Fig. 156), a species with a similar range to *O. instillatus,* and three more extend westwards across the subsaharan latitudinal belt as well, and one species, *O. flavus,* discussed above, occurs as a separate subspecies in southern Africa. This preponderance of species, coupled with a complete lack of West African endemics and the fact that most of the southern African species are closely related, suggests that the Somali peninsula has been the focus of speciation and radiation in the genus. Three members of Group I, one member of Group II, both of Group III, and the two ungrouped species all occur within this area. The species of group II have spread widely. *O. instillatus* is an East African endemic (Fig. 156), but *O. obtusangulus* (Fig. 156) occurs on the far side of the Red Sea in southern Arabia and has a smaller separate population in the mountainous region of Aïr in northern Niger. The remaining member of the group, *O. rosescens,* discussed below, is endemic to the Indo-Pakistan border area (Fig. 157).

The *Oedaleus* fauna of the subsaharan latitudinal belt

In his reviews of the Pleistocene in Africa, Moreau (1963; 1966) has shown that the Sahara has undergone far-reaching changes during the last 30 000 years. Plant and animal remains from the Ahaggar Massif 400 miles into the western Sahara indicate that Palaearctic elements were able to reach the centre of the desert during cool periods around 20 000–30 000 years ago, and even more recently Mediterranean vegetation apparently reached Aïr and Tibesti and possibly even further south. Ethiopian fauna also spread across the Sahara to North Africa during the late Pleistocene.

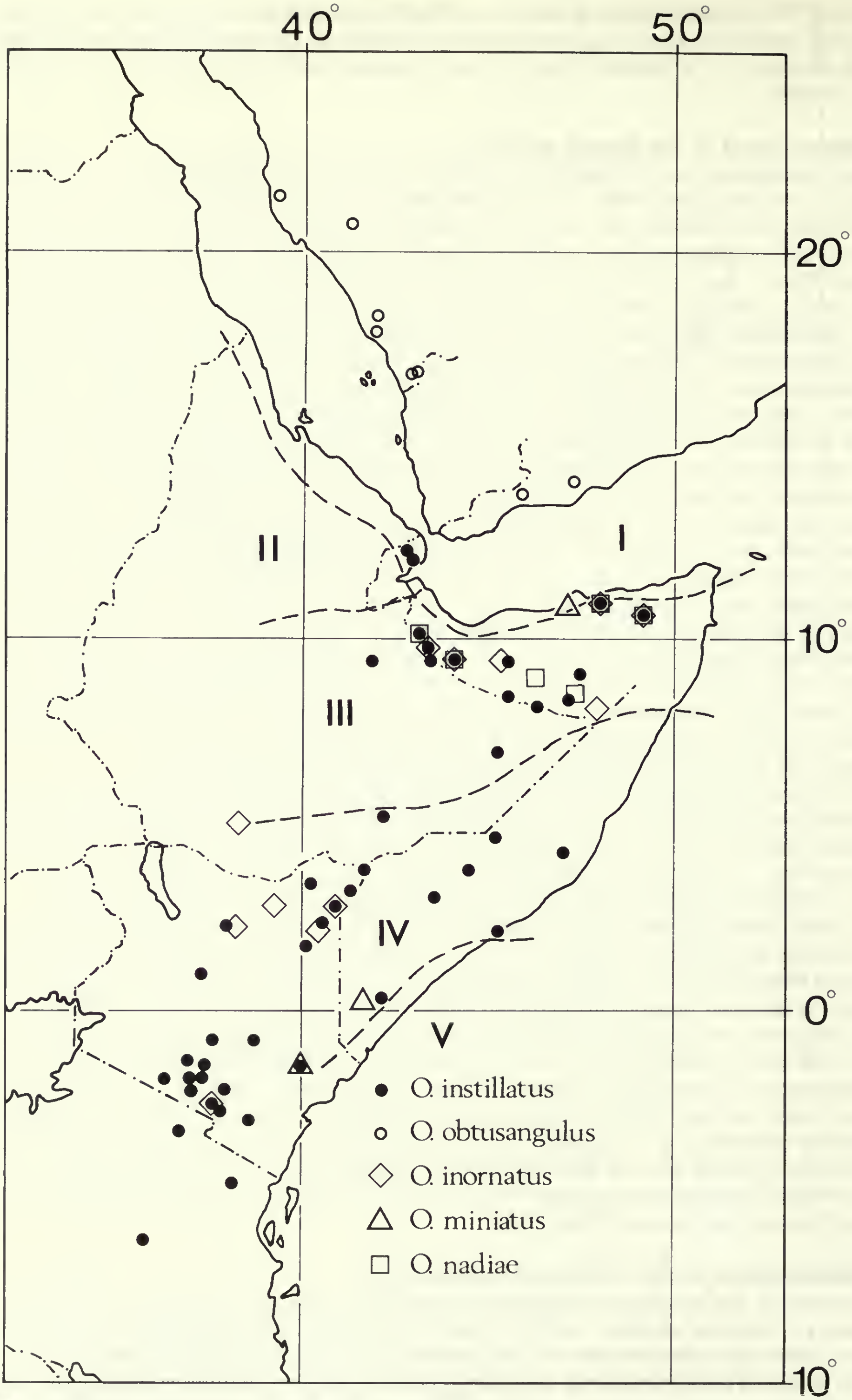

40°
50°
20°
10°
0°
10°
I
II
III
IV
V
● O. instillatus
○ O. obtusangulus
◇ O. inornatus
△ O. miniatus
□ O. nadiae

Fig. 156 Distribution of *Oedaleus* species in eastern Africa and south-western Arabia. Dashed lines with Roman numerals, climatic zones (Griffiths, 1972).

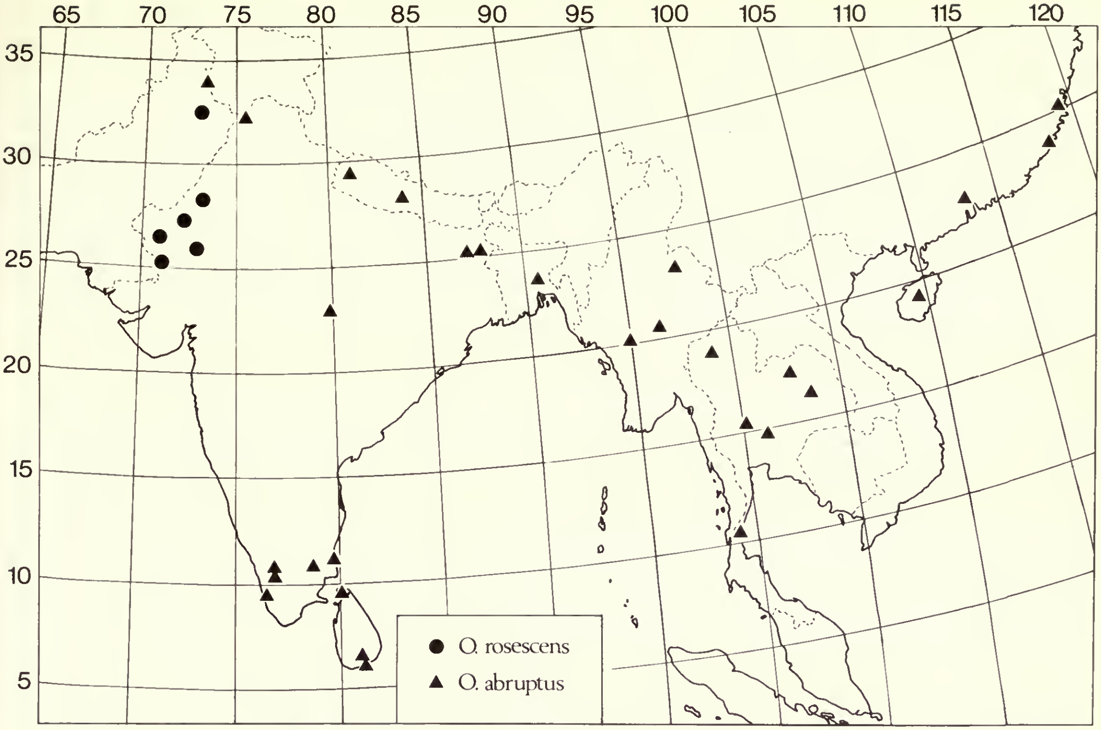


Fig. 157 Distribution of *Oedaleus* species in Asia.

From this Moreau concludes that at least in the western half of the Sahara there was during a period up until about 5000 B.P. no effective barrier to movement. From about that time Tibesti developed an Ethiopian flora, partly as a result of the great enlargement of Lake Chad between about 22 000 and 8500 years ago when it extended for 400 miles north of its present limit and was as large as the Caspian Sea. East of Aïr, at Adrar Bous, there existed about 8000 years ago a small lake in an area which is now sand desert. To the west of Aïr, Wadi Azouak, now a dry watercourse, was flowing around 5000 years ago, and, further west still, between Taoudeni and Timbuctoo, an inland basin fed by the upper Niger was forming a large lake (L. Arouane) which broke its eastward sill and drained into the lower Niger around 10 000 years ago. From this it may be seen that the western Sahara enjoyed a period of widespread climatic amelioration.

Van Zinderen Bakker (1969*b*), reviewing recent work on the Pleistocene and Holocene lake levels of the Sahara, indicates that their relationship to rainfall and temperature is very complex and warns against premature attempts to correlate all the available information into a simplistic model. He summarizes available dates for lake deposits into two groups between about 40 000 and 20 000 B.P. and between 12 000 and 3000 B.P. The earlier period is taken as indicative of the effect of the last glaciation which produced a southward movement of the Mediterranean rain belt and reduced the evaporation rate. The second period is coeval with the period of climatic amelioration after the glaciation which may have allowed the penetration of tropical rain from the south. However, the effect of the worldwide brief cold spell at around 5000 B.P. would have been to cause the tropical rain belt to move southwards again and the succeeding higher temperatures would have completed the desiccation which we see today.

These periods of climatic amelioration in the western Sahara during the last 40 000 years would have allowed the three species of *Oedaleus* which today have a subsaharan distribution to move northwards into areas which are now completely inhospitable. This may explain the presence of small populations of *O. senegalensis* in North Africa. *O. decorus,* the only other species of *Oedaleus* which occurs north of the Sahara today, is also a member of Group I and has become adapted to the winter rainfall Mediterranean zone (Fig. 158). If it originated in Africa south of the Sahara it is impossible to establish positively whether it entered Europe via the Middle East or from North Africa. The present discontinuous distribution of *O. obtusangulus* in SW. Arabia and Yemen and the Aïr mountains of Niger presumably represents a relic of a much wider continuous distribution during a time of climatic amelioration in the Sahara. This kind of disjunct distribution also occurs in *Truxalis longicornis* (Krauss), but it is surprising that Aïr should be the only known locality for *O. obtusangulus* in the Sahara since it only just reaches the lower altitudinal limit of montane conditions, whereas Tibesti and Ennedi, or even Ahaggar to the north, are much more substantial mountain refuges. It seems likely that the absence of *O. obtusangulus* from these areas is more apparent than real and that further populations will come to light. The lack of any discernible differences in morphology between the West African and Arabian populations indicates that this is a very recent disjunction.

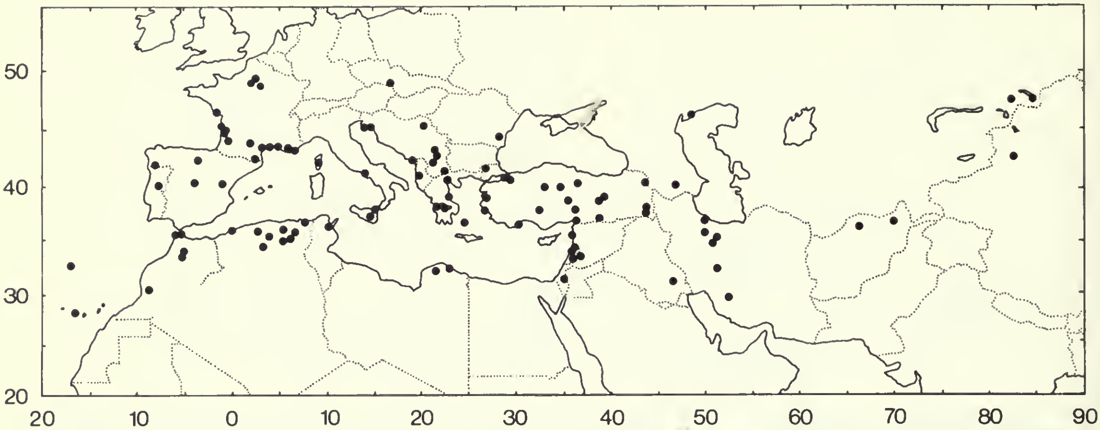


Fig. 158 Distribution of *Oedaleus decorus decorus* in north Africa, southern Europe, and western Asia.

While conditions in the Sahara itself were improved during the periods described above, paradoxically desert conditions moved southwards leaving a line of dead dunes 300 miles south of the present limit of moving sand (Fig. 159). It is known that this would have occurred around 20 000 B.P. at the height of the last glaciation, when the Mediterranean rainbelt moved towards the Equator (Hamilton, 1976). As a corollary of this advance of the desert, all the vegetation zones to the south must have shifted a corresponding distance and the forest would have been reduced to isolated patches.

These dramatic fluctuations of climatic conditions south of the Sahara doubtless account for the poor representation of grassland acridid species, including *Oedaleus,* when compared with eastern and southern Africa. The parallel arrangement of vegetation types from Senegal to Ethiopia has given rise to a corresponding distribution of *Oedaleus* species, of which the most northerly is *O. johnstoni.* This species is sporadically distributed across the subdesert steppe and Sahel savannah (Fig. 155) on silt and clay soils in wadis and on clay plains. In view of the mobility of the species, the unconfirmed record from Oman seems quite credible.

Further south (Fig. 160) *O. senegalensis* forms a broader, overlapping band across the Sahel and into the Somali peninsula. West of L. Chad the southern limit of this species corresponds closely with the belt of dead sand dunes mentioned above (Fig. 159). Isolated populations of *O. senegalensis* exist on both the Canary Is. and the Cape Verde Is. The Cape Verde population has given rise to a melanic form which is described and discussed elsewhere (Ritchie, 1978*a*). It is, however, of interest that according to Moreau (1966) the present day aridity of the islands has been exacerbated by human degradation of the original endemic vegetation since the discovery of the islands around AD 1460. This has now been reduced to inaccessible patches on cliff ledges. *O. senegalensis* may thus be a relatively recent invader though the eastern islands which are low and

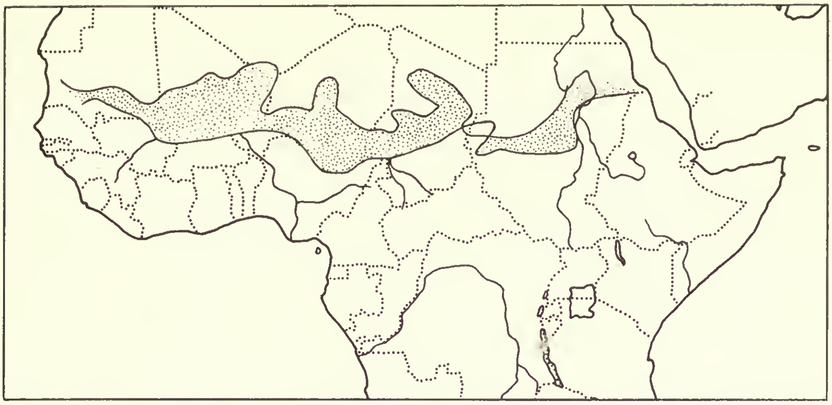


Fig. 159 The evidence for the southward advance of the Sahara during the late Pleistocene (after Hamilton, 1976). Stippled area, belt of fixed dunes.

sandy have probably always been more suitable for the species than the rocky western islands. Outside Africa *O. senegalensis* occurs around the fringes of the Arabian desert and northwards into the western U.S.S.R. and eastwards through Iran to India. An attempt has been made (Batten, 1969) to relate its distribution to the area between the mean annual isohyets of 10 and 40 inches. However, *O. senegalensis* is found in Arabia where the rainfall is less than 10 inches, and in India where it is in excess of 40 inches per annum.

The southernmost subsaharan range is that of *O. nigeriensis* (Fig. 161) which occupies a variety of vegetation types from the Sahel savannah through the *Isoberlinia* wooded savannah to the forest-savannah mosaic (Keay, 1959). In East Africa the species occurs in the moist woodland and savannah, particularly in Uganda, and south of the Equator it is found throughout the *Brachystegia* woodland, penetrating as far as southern Zambia. At this point, around 15°S, the mopane wooded savannah recommences and *O. nigeriensis* is replaced by *O. carvalhoi*.

The non-african *Oedaleus* fauna

The species of *Oedaleus* found outside Africa are, as stated earlier, either identical with, or closely related on morphological grounds to those of Africa. Madagascar possesses one very widespread endemic species, *O. virgula* (Fig. 162), of which there is one old specimen labelled as from Zanzibar. This record is remarkable if it is genuine since the two islands are well separated and *O. virgula* is not known from Grand Comoro which lies between. Instead *O. nigeriensis* occurs on this island but not on Zanzibar which is much closer to the mainland of Africa and was only separated from it around 10 000 years ago (Moreau, 1966). There is one other old specimen of *O. virgula* labelled as from the Cape, but this can almost certainly be attributed to mislabelling. Very recently Dr N. Waloff has discovered this species on the island of Aldabra, indistinguishable from the Madagascar population. It may well occur on other islands also.

In mainland Asia there are four endemic species of *Oedaleus*. *O. rosescens*, a member of Group II mentioned above, was previously known only from the desert area of NW. Rajasthan and the Salt Range of NE. Pakistan, on the border of another desert area, but it has recently been collected west of the mouths of the Indus at Landhi, near Karachi (Fig. 157). The habitat of this species is probably similar to that of *O. instillatus*, a related species in East Africa, though possibly more arid. Further east *O. abruptus* (Fig. 157), a small species in Group I, has a wide range in the tropical grasslands of southern Asia in lowland areas south of the Himalayas. This species was recently introduced into the island of Oahu in the Hawaiian Is., presumably on United States aircraft returning from SE. Asia to Hickam Air Force Base, Honolulu (U.S.D.A., 1968). Despite eradication attempts the species has now spread to Kauai island more than 100 miles to the west (U.S.D.A., 1976). To the east of the Himalayas *O. infernalis* occurs widely (Fig. 163) in southern and eastern China and into Korea and the extreme south-east tip of the U.S.S.R., in areas with an annual rainfall of between 20 and 60

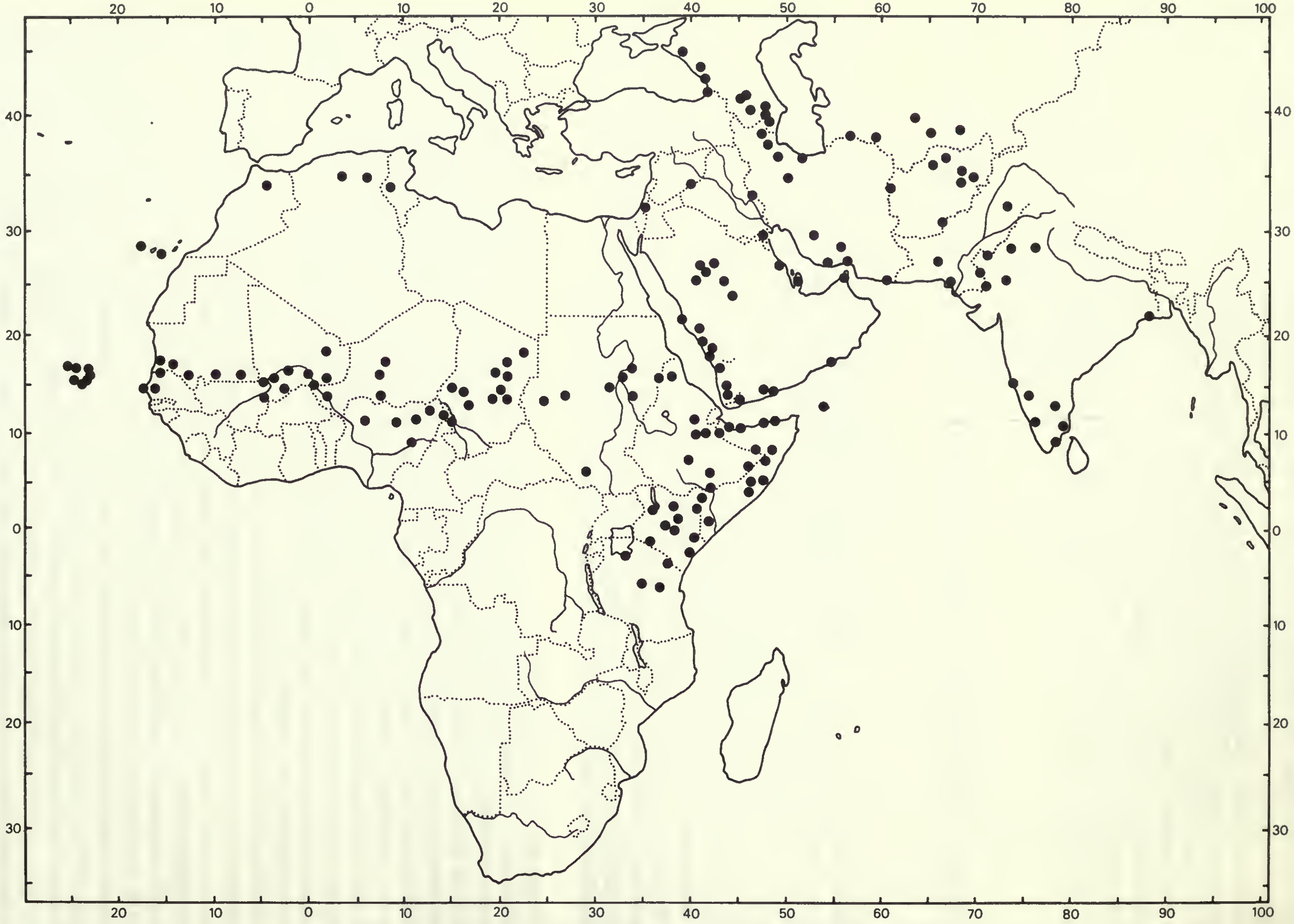

20
10
0
10
20
30
40
50
60
70
80
90
100
40
30
20
10
0
10
20
30

Fig. 160 Distribution of *Oedaleus senegalensis* in Africa and western Asia.

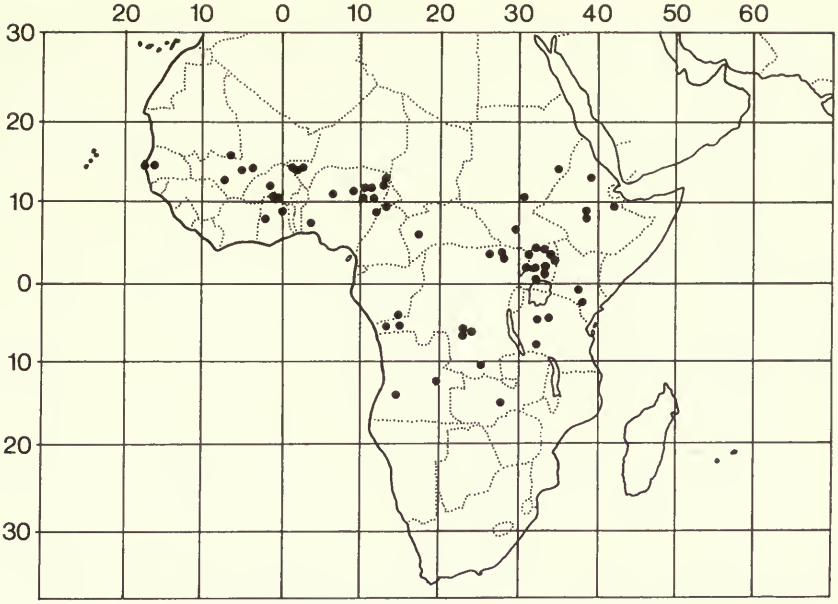


Fig. 161 Distribution of *Oedaleus nigeriensis* in Africa.

inches. This species also occurs in the southern half of Japan, but in Taiwan it is replaced by *O. formosanus*, a little-known related species which appears to be restricted to montane areas (Fig. 163). North of the Himalayas *O. decorus asiaticus* (Fig. 163) is distributed in the western Sayan Range and the Transbaikal region of the southern U.S.S.R., and in Mongolia, with a south-eastward extension into Hopeh and Shantung provinces of China. Much of the range of this subspecies is montane and winter conditions, particularly at higher latitudes, must be very severe.

The furthest point reached by *Oedaleus* is the continent of Australia where one species, *O. australis*, occurs widely in the eastern half of the continent (Fig. 164), apparently independent of vegetation type or altitude but correlated to some extent with areas having an annual rainfall in excess of 10 inches. In the Northern Territory it is probable that the species extends further west than is known at present, but the human population density is low and the area is less well collected than the eastern half of the continent. The absence of *O. australis* from the south-western corner of Western Australia suggests that the species has arrived since the height of the last glaciation when there was a corridor along the south coast between the desert and the sea, formed by the fall in sea level which took place in the Great Australian Bight. This is known to have provided a means of access for non-desert animals to reach the area at that time which have since evolved in isolation from the populations to the east of the desert (W. Bailey, pers. comm.). The single record of *O. australis* from Port Moresby, New Guinea, is a possible indication of the route by which *O. australis* may have reached Australia. However, Key (pers. comm.) suggests that this may be a recent introduction. Parts of the south coast of New Guinea are quite dry but at present no other suitable sites for *O. australis* exist. Presumably New Guinea and the Indonesian Archipelago must have been the bridge by which *Oedaleus* reached Australia, but this could only have been possible at a time when these islands experienced a much drier climate than at present. Whyte (1968) brings forward the lowering of sea level at glacial maxima and the consequent increase of land surface as a possible desiccating factor. However, the decline in precipitation occasioned by the glaciation itself seems a more probable cause of the spread of drought-adapted biota through areas like Malaya, Sumatra, Borneo, and New Guinea which are today mainly covered by rain forest. According to Whyte south New Guinea and Australia have many xerophytic plants which are identical to those of mainland Asia and their immigration is therefore believed to be recent. An alternative but less likely explanation of the presence of *O. australis* on the far side of a barrier of humid forest would be that it evolved from a form which was initially tolerant of high humidity but became more xerophilous after invading Australia. However, against this suggestion stands the complete absence of any species of *Oedaleus* anywhere between Thailand and New Guinea today. Instead this region has been the setting for a minor radiation of *Gastrimargus* species, a group which throughout its range is consistently more tolerant of humid habitats than *Oedaleus*.

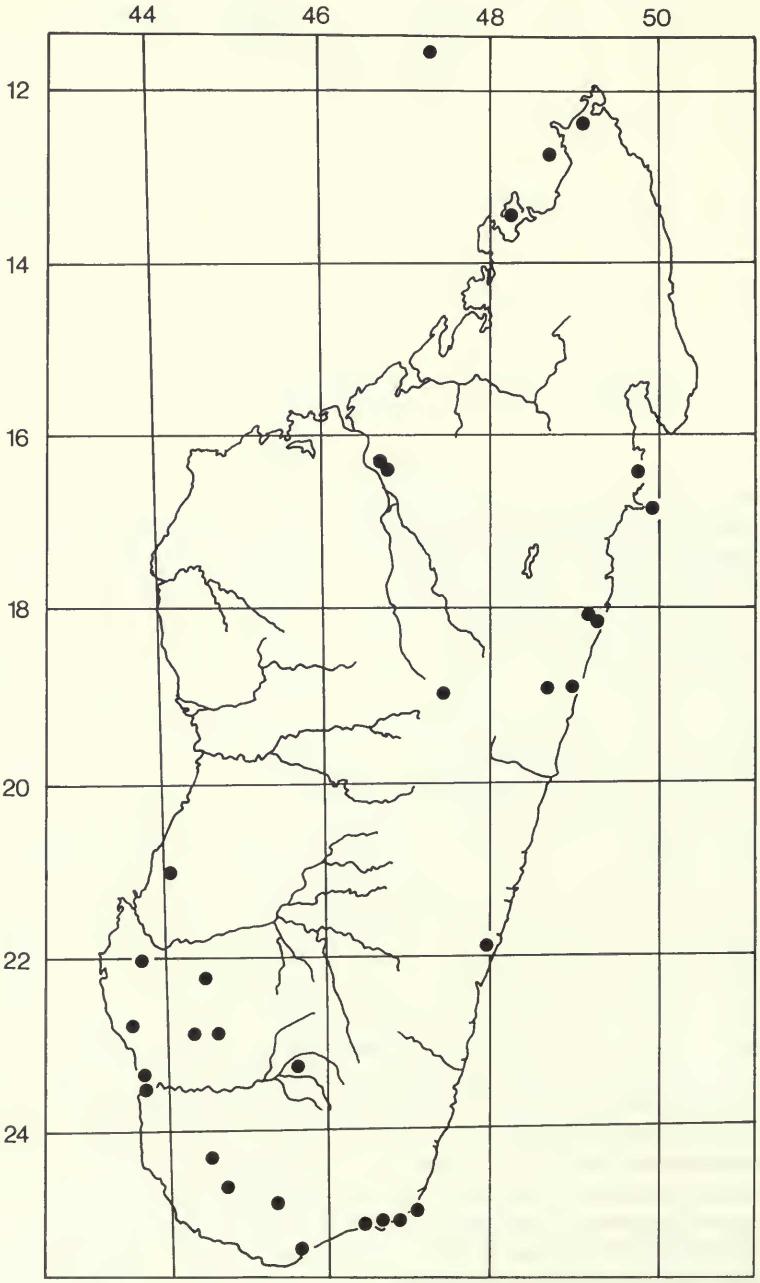


Fig. 162 Distribution of *Oedaleus virgula* in Madagascar.

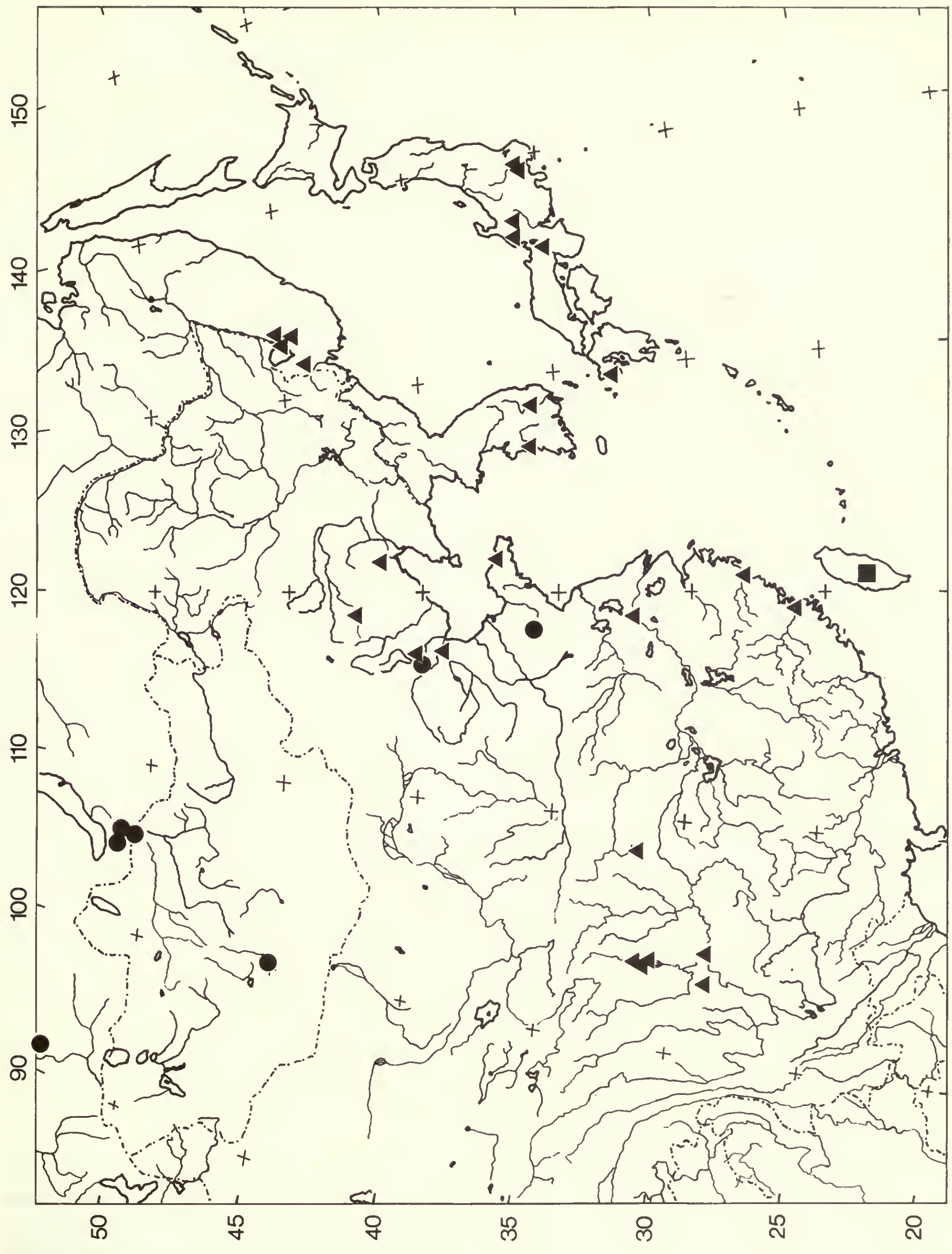

150
140
130
120
110
100
90
50
45
40
35
30
25
20

Fig. 163 Distribution of *Oedaleus* species in eastern Asia. Circles, *O. decorus asiaticus*; triangles, *O. infernalis*; squares, *O. formosanus*.

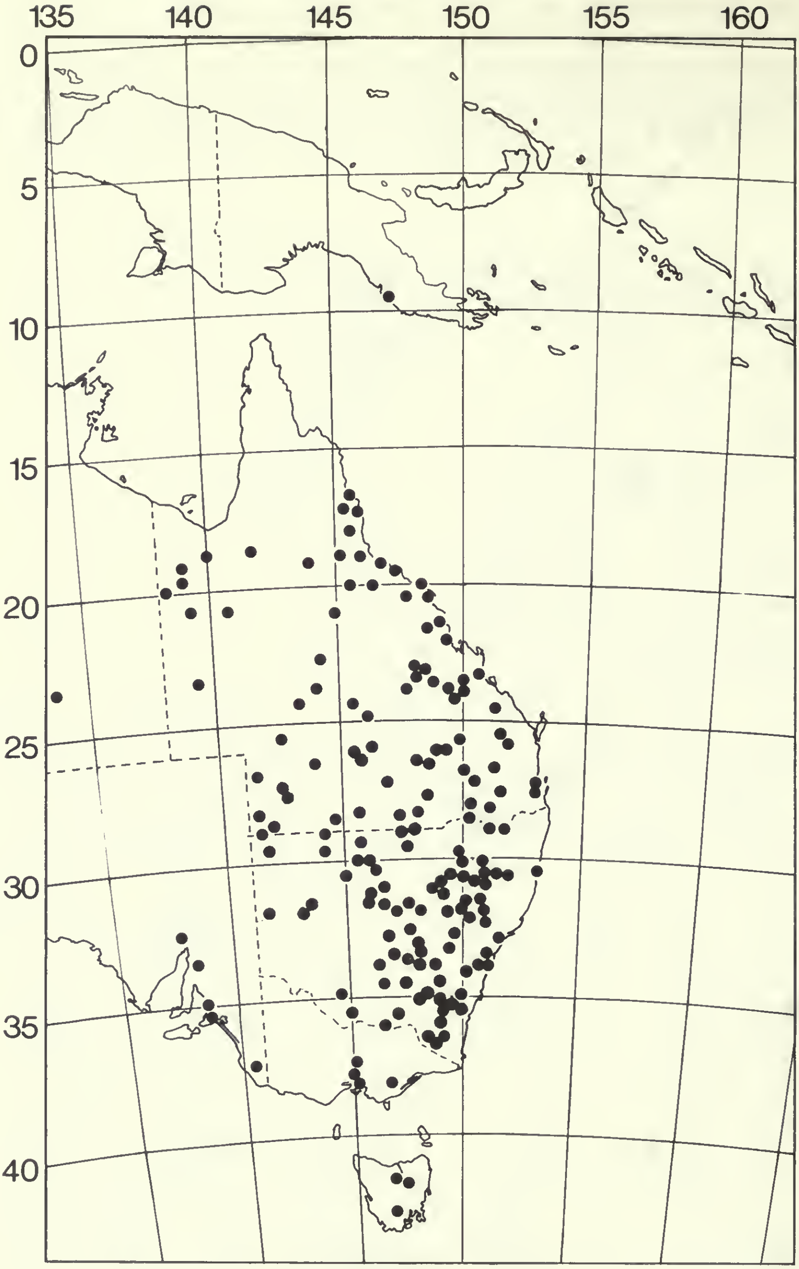


Fig. 164 Distribution of *Oedaleus australis* in Australasia.

Problems of analysis of distribution patterns
In discussing the distribution of a large (by the standards of the Acridoidea) genus of mobile savannah grasshoppers there are several difficulties. Firstly, there are relatively few other large genera with similar ecology which have recently undergone revision. La Greca (1970) has shown how ideas of the distribution of the Mantodea have been radically altered after comprehensive revision of the taxonomy of the group. Secondly many species of acridids are of rather infrequent occurrence despite wide ranges, and thirdly many distribution maps are based upon an inadequate coverage of the areas treated simply because collections have not been made. Representation of the

genus *Oedaleus* in collections is probably above average because of the tendency to high population levels in many species and their concentration in the marginal agricultural areas of the Old World tropics and subtropics where locust control organizations have worked extensively.

East African acridid diversity

In the above analysis, it has been inferred (p. 159) that *Oedaleus* is of East African origin, and that this is an outcome of the relative climatic stability of the area during the Pleistocene, its partial isolation both then and now, and its present ecological diversity. This is a familiar pattern of distribution since there are at least 114 genera of African grasshoppers which have some representation in East Africa. Of these 42 are endemic to the area, and 26 of those are monotypic genera. This is a very conservative estimate based on Johnston (1956; 1968) without including genera known from Tanzania unless they are also recorded from further north. Genera known from the islands off the coast of Africa are also excluded in the same way. No attempt has been made to supplement Johnston's information from more recent published or museum sources. Such a survey, to be accurate, would require the revision of all the genera of African grasshoppers. For the purposes of this study it may safely be assumed that there are more described genera represented in East Africa than the figures quoted suggest. There are also undescribed genera from Somalia in the BMNH which would swell the list still further.

As indicated above (p. 159), the *Oedaleus* fauna of West Africa is much poorer than that of East Africa and entirely lacks endemic species. This is a reflection of the comparatively rather low degree of endemism among subsaharan savannah grasshoppers in general. It is, however, surprising that although *O. senegalensis* is found on both sides of the Ethiopian Highlands *O. instillatus* only occurs to the east although it is a widely distributed, mobile, xerophilous species. Quite possibly the rather more uniform topography and vegetation of the subsaharan latitudinal zones do not offer sufficient habitats for more than the three which are found there. In addition, despite the fluctuations of climate already mentioned, the mountains of Ethiopia and the deserts on the Eritraean coast and around Lake Turkana (L. Rudolph) must have constituted formidable barriers to any westward expansion by the East African biota. Monod (1971) has noted a parallel case of poor subsaharan representation in the genus *Commiphora,* one of the characteristic plants of Keay's (1959) category 'wooded steppe with abundant *Acacia* and *Commiphora*'. Compared to a total of about 80 East African species West Africa has only five. Monod also notes the surprising absence of the gnu and the zebra from the West African savannah.

The *Brachystegia* woodland and 'trans-equatorial' speciation

It is apparent from the account of the distribution of *Oedaleus* in Africa given above that the genus divides into different subspecies or species to north and south of the Equator. This kind of distribution pattern is very common in acridids and Jago (1973) has formulated a hypothesis to account for it. According to this theory savannah grasshoppers having an adult diapause initiated by decreasing daylength north of the Equator are out of step with those on the southern side because the daylength and rainfall regimes are six months out of phase. Hence speciation can occur since sexually mature adults on either side of the Equator never meet. The hypothesis is based upon the known mechanism of photoperiodic diapause-induction in *Nomadacris* Uvarov and *Anacridium* Uvarov as studied in the laboratory (Norris, 1959; 1965*a*; 1965*b*). However, as Tauber & Tauber (1976) have said in their recent review of insect seasonality: '. . . to establish when reproduction will begin in the field it is generally necessary to know when diapause ends *in nature* [my italics]. However answers to this problem are usually not well substantiated even for species whose diapause has been studied'. Much field and laboratory work has been done with *Nomadacris* from the Rukwa valley, south of the Equator, and a little on material from the Niger flood plain, north of the Equator. In both areas onset of diapause coincides with changing photoperiod (Uvarov, 1977: 305), and theoretically there would be no time overlap in the breeding period to permit interbreeding. However, termination of diapause in *Nomadacris* may well be effected by temperature change or rainfall (Robertson, 1958), and it is possible that a trans-equatorial migrant would be able to synchronize with the resident population at whatever stage was appropriate. In any event the species appears to have a continuous range from Somalia to South

Africa without any discernible morphological hiatus at the Equator so it cannot at present be considered as offering material support to a belief in an 'Equatorial Species Dynamo'.

Another factor which tends to weaken the general applicability of a specifically trans-equatorial mechanism is the prevalence of egg rather than adult diapause in Acridids. For example, 13 out of the 51 species of Sudanese Acridoidea investigated by Joyce (1952) survive the dry season in the egg stage. In species such as these the initiation of diapause may be in response to changing day length, but this response gradually weakens in preparation for post-diapause development (Tauber & Tauber, 1976), and once again the actual trigger for development to recommence may simply be rainfall. In *O. senegalensis* in India there is evidence that rainfall between six months and one year after laying is sufficient to break diapause (Venkatesh *et al.*, 1971). The occurrence of intercalary hatching in December, 1961 in the Cape Verde Is., in response to unusually heavy rain (Saraiva, 1962; Batten, 1969), may indicate that eggs can hatch soon after laying, even at the end of the season when they would normally diapause. Clearly, if photoperiod does influence egg diapause in *O. senegalensis*, the influence is on its induction and may be weak and of short duration. A trans-equatorial migrant of this species would presumably have no difficulty in adjusting to the new seasonal timing.

Jago (1973) has pointed out that *Locusta* in Africa cannot exist at high population densities after invading areas south of the Equator. However, this species appears unable to maintain high densities anywhere else either, apart from the main outbreak area in the flood plain of the Niger. There are in fact many species which do succeed in spanning the Equator apparently without alteration (e.g. *Dnopherula cruciata* (Bolívar), *Humbe tenuicornis* (Schaum), *Trilophidia conturbata* (Walker)) though there is always the possibility of unrecognized cryptic speciation. The most well-studied example of this phenomenon concerns *Eyprepocnemis plorans* (Charpentier). This species was divided by Dirsh (1958) into several 'subspecies' of which *E. p. ornatipes* (Walker) and *E. p. meridionalis* Uvarov are found to the north and south of the Equator respectively. John & Lewis (1965) demonstrated meiotic breakdown in hybrids between these 'subspecies', indicating that speciation had occurred. No F_2 generation hybrids could be produced. There is, however, no direct evidence that this was directly attributable to trans-equatorial effects. *E. p. ornatipes* is apparently not found nearer to the Equator than northern Kenya, while *E. p. meridionalis* in the south penetrates northwards as far as 3°S on the west but only about 7°S in the east of Tanzania. Remarkably, the intervening area is occupied by a hybrid not between these two species or subspecies, but between *E. p. meridionalis* and *E. p. plorans*, the Mediterranean form. Clearly this is a rather complex situation, but one feature of it, the diagonal northern boundary of the *E. p. meridionalis* zone just south of the Equator in N. Tanzania, recurs time and time again in the distribution of African acridids and is particularly noticeable in *Oedaleus*. Examples of northern species which show a discontinuity at this point are *O. senegalensis, O. flavus somaliensis, O. instillatus*. All these cross the Equator but are apparently unable to advance across the *Brachystegia* woodland zone, within which the only species of *Oedaleus* found is *O. nigeriensis*.

In *Aiolopus simulatrix* (Walker), a member of a related genus revised by Hollis (1968), there is a good example of subspeciation exactly at the northern boundary between the savannah and woodland. On the savannah side of the boundary occurs *A. simulatrix simulatrix*, and on the woodland side to the south is found *A. s. femoralis* Uvarov. Some acridid species, including *O. plenus plenus* and *Aiolopus meruensis* Sjöstedt, occur both north and south of the barrier apparently unaltered, but are never found within the woodland itself. Other species are split into subspecies or species pairs either at the savannah/woodland boundary or across the width of the woodland barrier itself. The major examples of these effects have been described above. Keay (1959) has pointed out the importance for grasshoppers of 'ecotones and mosaic habitats in which the scale of the patchwork is adjusted to the vagility of the species'. In *Acorypha* Krauss, a genus of grasshoppers of rather low vagility, speciation has occurred in response to quite small scale geographical features. This has perhaps been assisted by ecological specialization and the variability of genital morphology allowing pre-mating isolation of newly diverged forms. Only in one species, *A. glaucopsis* (Walker), is there a clear separation at the savannah/woodland boundary, regarded by Jago (1973) as a delayed response to the Equator. *Oedaleus* and *Aiolopus* on the other hand are both xerophilous genera of high vagility requiring as a rule wide separation to prevent continual reinvasion of disjunct populations. This is particularly true in view of the low level of interspecific variation both in ecology and in genital morphology. The suddenness of specific and subspecific discontinuities and the number of species in which they may be observed, are strong evidence in favour of the view that speciation among the more xerophilous savannah grasshoppers occurs not at the Equator but on the northern and southern boundaries of the *Brachystegia* woodland, which constitutes a barrier of no less than 500 miles at its narrowest point, and effectively much wider, particularly when the Southern Highlands of Tanzania are added to the problems encountered by migrant insects.

The woodland barrier and the 'arid corridor': evidence from other groups

The evidence for the importance of the *Brachystegia* woodland barrier in the evolution of the Acrididae discussed above is strongly reinforced by recent biogeographical studies of other groups of animals and plants. The affinities between the biota of the arid and semi-arid regions of south-western and north-eastern Africa have been noticed by many biologists and in recent years several of them have suggested that there must have been a former link between the two areas. For example Monod (1971) has shown that of 556 genera of flowering plants occurring in the Sahel 354 (63%) also occur in the southern savannah. Balinsky (1962) has indicated the existence at the present day of an 'arid corridor' joining these regions which could be defined in terms of a rainfall of less than 10mm per month during at least three consecutive months (Fig. 165). The disjunct distribution patterns of large numbers of plants and animals suggest that, for them at least, the arid corridor is no longer effectively open and that the belt of *Brachystegia* woodland now constitutes a complete barrier between the more arid regions north and south. Monod (1971) found that out of 84 genera of flowering plants analysed 50 had disjunct north/south distributions. Forty species of plants and two species of coprophilous fungi were found to occur in the northern and southern arid zones but nowhere in between, and Lebrun (1971) has described four more cases of flowering plants with the same disjunct range. De Winter (1971) noted that in the Poaceae alone there were 17 species with discontinuous distributions in the northern and southern arid areas.

Discussing the resemblances of the bird fauna of north-east and south-west Africa, Winterbottom (1967) has estimated that there are 205 species in the south-west arid zone and 133 in the former British Somaliland and the Gulf of Aden. Of these about 30 species are held in common either as the same or different subspecies, species pairs, or close relatives. From this analysis Winterbottom reached the following conclusions: 1, the necessity of a past connection between the arid faunal areas of Chapin (Fig. 166); 2, the different degrees of differentiation between northern and southern populations suggest that there has been more than one period when the corridor was open; 3, the high degree of endemism in the two areas suggests that the link between them has been of brief duration or incomplete, or both. He makes the suggestion that the link would have followed the Luangwa valley which at present carries more open vegetation north-eastwards far into the *Brachystegia* zone. Even today several southern bird species penetrate northwards along this valley to within 150 miles of the dry wooded steppe of NE. Tanzania which advances south along the valley of the Great Ruaha river.

Among mammals also there are striking examples of disjunct distribution which suggest the existence of a former connection between the northern and southern arid zones. Roberts (1937*a*; 1937*b*) noted the discontinuous ranges of the dik-dik, *Madoqua kirki,* which has a south-western subspecies *damarensis* (Monod, 1971), and of the oryx, which forms a species pair with *Oryx gazella* in the south-west and *O. beisa* in the north-east (Meester, 1965). Meester has also noted further examples including the bat-eared fox, *Otocyon megalotis,* occurring in both arid regions, and the gerbil which has two closely related species in the two areas. Bigalke (1968) has estimated that the Somali peninsula has about 15 endemic mammals and notes the occurrence of a distinct species of hartebeest, *Alcelaphus lichtensteinii,* in the *Brachystegia* zone separating different subspecies of *A. buselaphus* in the north-eastern and south-western arid areas. As further evidence of a past corridor Verdcourt (1969) has stated that fossil material of the gerenuk, 'a typical Somali thornbush antelope extending into N. Tanganyika' has been found at Broken Hill in Zambia, an area presently surrounded by *Brachystegia* woodland.

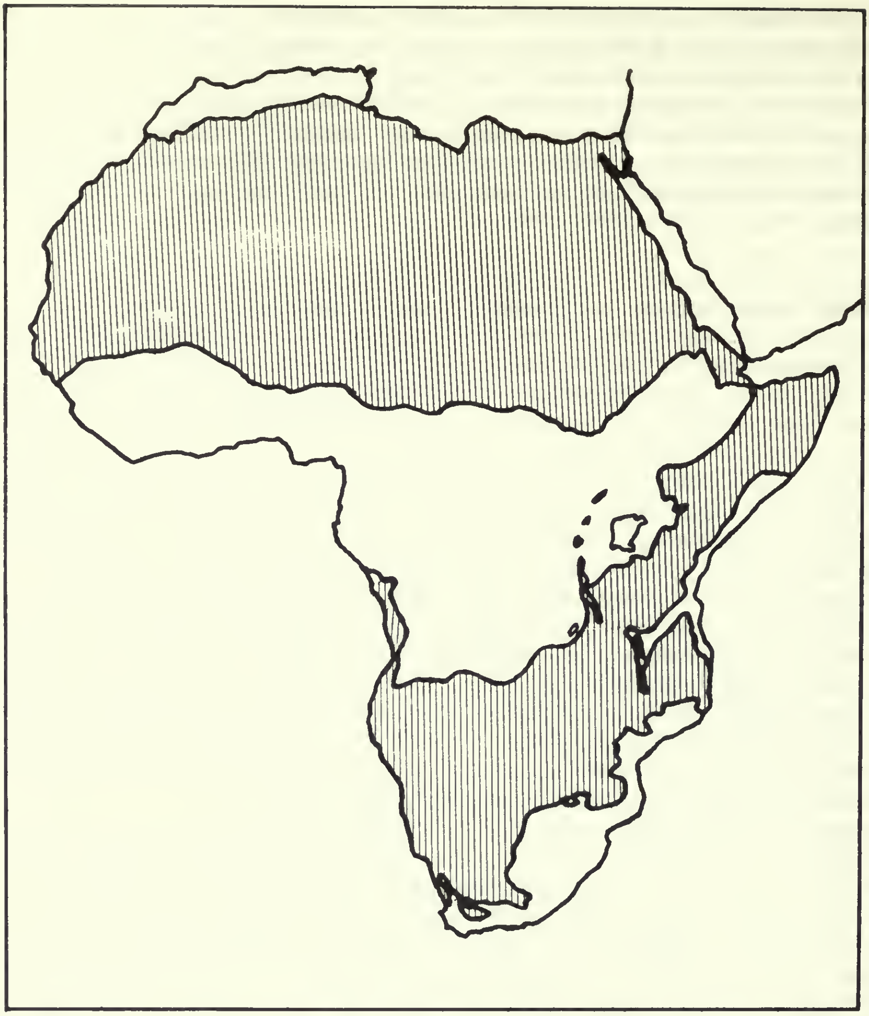


Fig. 165 Distribution in Africa of arid regions having less than 10 mm of rainfall per month during at least three consecutive months (after Balinsky, 1962).

Bigalke (1968) considers the observed overlap of some woodland mammals into arid areas as encroachment. However, they could also be regarded as relicts of former woodland extensions. For example Davis (1962) has noted that several southern African species of Muridae which avoid arid areas reach as far north into the savannah as the Tana river watershed in southern Kenya, a level known to zoogeographers as 'Sclater's Line'. Kingdon (1971) suggests that a past extension of the Congo forest eastwards from the north of L. Victoria to Sclater's Line was responsible for the racial divisions of hartebeeste and savannah monkeys (*Cercopithecus*) to the north-east and south-west. Even under present day conditions one may see from the vegetation map of Africa (Keay, 1959) that there is a considerable barrier to movement of lowland savannah biota across this mosaic of lakes, montane forest, and moist woodland. An additional isolating factor already mentioned above (p. 159) in relation to latitudinal movements, but equally important in impeding north-south mobility, is the desert and subdesert extending south-eastwards from L. Turkana. If it is certain that forest and woodland have on occasions formed an effective barrier under extreme pluvial conditions, it is at least probable that under conditions of increased aridity the Turkana desert would have enlarged sufficiently to impede the migration of less xerophilous biota.

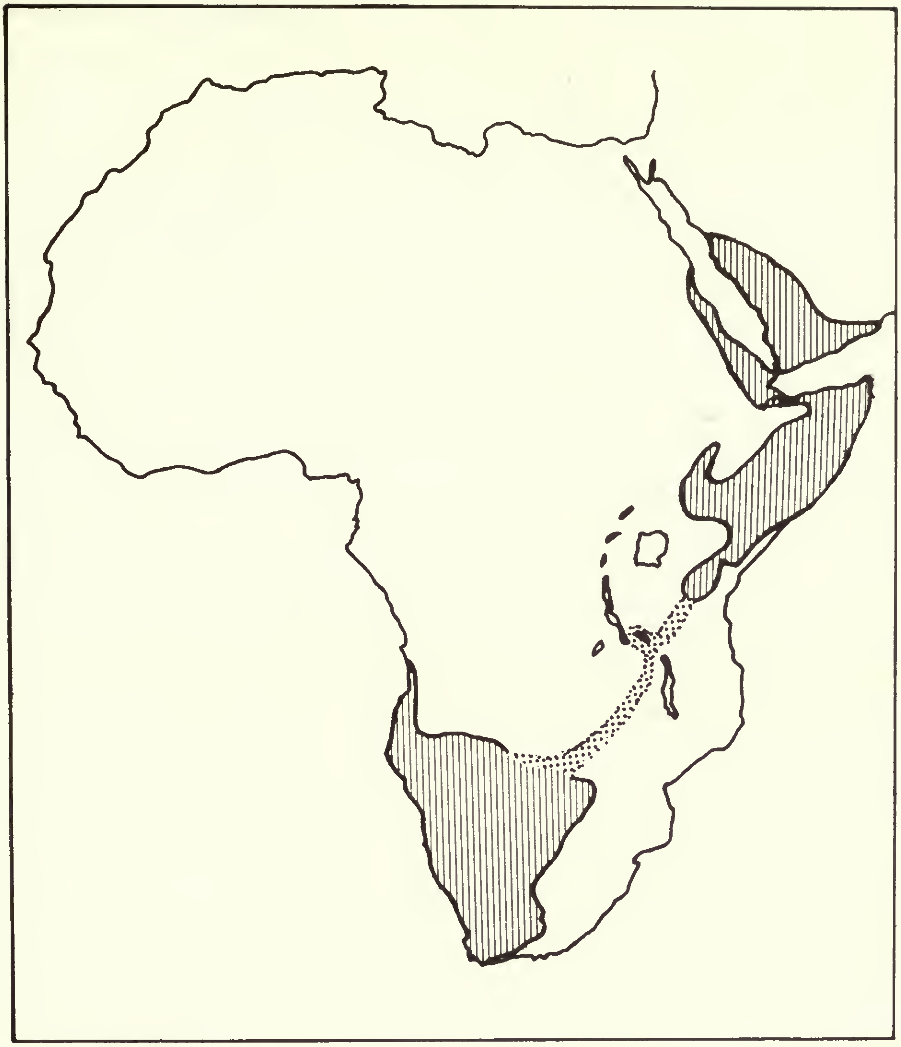


Fig. 166 Outline map of Africa showing Somali Arid and South West Arid Districts (vertical lines) and the suggested past corridor between them (dots) (after Winterbottom, 1967).

Among entomologists the faunal links between the northern and southern arid zones have apparently received relatively little attention. Koch (1960) has noted the similarities between the Tenebrionid beetle faunas of the Namib desert and the deserts of northern and eastern Africa and even Asia at the tribal level. The extensive and often sympatric speciation in the Namib and the very high degree of specific endemism indicate an ancient union of this area with other deserts in Africa and Asia. However, this could only have resulted from an earlier, more sustained, and more extensive period of aridity than that being postulated here as responsible for the reunion of semi-arid rather than true desert biota. In the Rhopalocera Carcasson (1964) has shown that north-east/south-west speciation is rare since butterflies are essentially insects of forest and woodland which have not extensively colonized the more open vegetation zones. However, there are minor centres of speciation within the *Brachystegia* woodland and in the north-east arid zone. By contrast to the Tenebrionidae, the butterflies have no centre of radiation within the south-west arid zone. There are, however, disjunct north/south distributions in the genera *Dixaea* and *Colotis*. Carcasson notes that even those species of *Colotis* which are tolerant of woodland have undergone speciation as a result of a past eastward extension of the forest.

This brief review of recent literature indicates a growing awareness of the rôle of the *Brachystegia* woodland barrier in the evolution of the savannahs and steppes of Africa, and the past existence on one or more occasions of an arid corridor between the north-eastern and south-western semiarid zones. In addition to this biogeographical evidence there is a growing body of palaeoecological data to assist in reconstructing the changes in the climate and vegetation of Africa during the late quaternary. A useful summary has been given by Van Zinderen Bakker (1976) whose theoretical reconstruction of the vegetation of subsaharan Africa has been mentioned earlier (p. 154 & Fig. 151). In this review (p. 174) Van Zinderen Bakker concludes that during 'dry glacial times . . . the 'arid corridor' . . . would have been open'. However, in an earlier paper (1969*c*: 139) he had suggested that 'present-day rainfall maps show that a corridor . . . probably existed during periods with a higher temperature'. He added that pollen analyses at Kalambo Falls at the southern end of L. Tanganyika show that 'conditions could have been hot and dry in the gap between the Ufipa Plateau and the Malawi Mountains during one of the warm interstadials or during the postglacial temperature optimum'. Hamilton (1976) puts the case for the fragmentation of the Congo forest during at least the period of the last glacial maximum between 25 000 and 12 000 B.P. and suggests that the forest may not previously have been continuous across the Congo basin until as far back as 75 000 B.P. During some part of this period the East African arid corridor was presumably open, at least partially or intermittently. In an earlier review of the subject Moreau (1966) had put forward the theory that montane forest would have descended from about 1500 m to 500 m at the last glacial maximum, isolating lowland savannah biota in widely separated refuges, but this has since been rejected as unrealistic (Van Zinderen Bakker, 1975).

Conclusions

From the above it will be apparent that the exact timing and duration of any past breaches in the woodland barrier, and the degree of contact between north and south that they afforded, are still matters for discussion. What now seems certain, however, is that the *Brachystegia* is an effective isolating mechanism at the present time, and that it has been breached by a corridor of more open vegetation one or more times in the past. The effect this has had on the flora and fauna of Africa is becoming steadily clearer. In the Acridoidea the cyclical separation and reunion of the eastern and southern savannahs explains much of the observed speciation and subspeciation in xerophilic genera. In view of the subtlety of the morphological changes which often accompany this evolutionary process there is a need for thorough revision of savannah genera with more attention to biogeographical considerations. The possibility that cryptic speciation may occur in disjunct populations of acridids highlights the importance of cytogenetic studies like those of John & Lewis (1965) on *Eyprepocnemis plorans* as a necessary back-up to morphological methods. The more precise understanding of the taxonomic status of grasshopper populations which could be gained by such studies would be of practical service in the control of pest species by indicating whether biological data which have been gained, for example, from northern populations of a species are likely to have only limited application to southern populations.

Acknowledgements

This revision forms part of a thesis approved by the University of London for the degree of Doctor of Philosophy. I am most grateful to my Supervisor, Dr N. D. Jago, and my Director of Studies, Dr N. Waloff, for their advice and encouragement throughout the course of this study.

I am indebted to the Trustees of the British Museum (Natural History) and the Keeper of Entomology for access to the collections which form the basis of this work, and to the following individuals for the loan of specimens and other assistance: Dr S. Asahina (Tokyo), Dr H. D. Brown (Pretoria), Dr P. Basilewsky (Tervuren), Dr F. Capra (Genoa), Dr G. Demoulin (Brussels), Dr P. H. van Doesburg (Leiden), Dr M. Donskoff (Paris), Dr J. de A. Fernandez (Lisbon), Dr K. K. Günther (Berlin), Dr A. Gurney (Washington), Dr L. Hedström (Uppsala), Dr B. Hauser (Geneva), Mr J. Houston (Church Stretton), Dr P. Johnsen (Aarhus), Dr A. Kaltenbach (Vienna), Dr K. H. L.

Key (Canberra), Dr T. Kronestedt (Stockholm), Dr G. Messana (Florence), Dr L. L. Mishchenko (Leningrad), Dr D. Rentz (San Francisco), Dr D. Otte and Dr H. R. Roberts (Philadelphia), Mr E. Taylor (Oxford).

References

Abushama, F. T. & El Khider, E. T. M. 1973. Colour change in the grasshopper *Oedaleus senegalensis* Krauss (Fam. Acrididae). *Z. angew. Ent.* **72:** 415–421.

Adamovic, Z. R. 1968. Feeding habits of some robber flies preying upon Orthoptera. *Ekologija. Beograd.* **3:** 119–132.

Adamson, R. S. 1938. *The vegetation of South Africa.* ix + 235 pp. London.

Ahmed, M., Irshad, M. & Ali, R. 1973. Natural enemies of grasshoppers in Pakistan (for the U.S.A.). *Rep. Commonw. Inst. biol. Control* **1972:** 59–60.

Amedegnato, C. 1976. Structure et évolution des genitalia chez les Acrididae et familles apparentées. *Acrida* **5:** 1–15.

Asana, J. J., Makino, S. & Niiyama, H. 1939. A chromosomal survey of some Indian insects. II. A comparative study of the chromosomes in six species of Acrididae. *Jap. J. Genet.* **15:** 251–260.

Balinsky, B. I. 1962. Patterns of animal distribution on the African continent. *Ann. Cape prov. Mus.* **2:** 299–310.

Ballard, E. 1914. A list of the more important insect pests of crops in the Nyasaland protectorate. *Bull. ent. Res.* **4:** 347–351.

—— 1921. Additions and corrections to the list of crop-pests in south India. *Rep. Proc. 4th ent. Meet. Pusa* **1921:** 21–28.

Barber, M. A. & Jones, C. R. 1915. A test of *Coccobacillus acridiorum* d'Herelle on locusts in the Philippines. *Philipp. J. Sci.* **10**(B) 2: 163–176.

Barbut, M. 1954. Parasites à charactère migrants. I.-Acridiens. *Rapp. Cons. Exp. Rech. agron. Algér.* **1933:** 338–339.

Batten, A. 1969. The Senegalese grasshopper *Oedaleus senegalensis* Krauss. *J. appl. Ecol.* **6:** 27–45.

Bei-Bienko, G. Ya. 1941. [New or little known Orthoptera discovered in U.S.S.R.] [In Russian.] *Zap. leningr. sel'.-khoz. Inst.* **no. 4:** 147–159.

—— 1951. *In* Bei-Bienko, G. Ya. & Mischenko, L. L., Acridiodea of the U.S.S.R. and adjacent countries. Part II. [In Russian.] *Opred. Faune SSSR* **40:** 1–286.

Bei-Bienko, G. Ya. & Mishchenko, L. L. 1951*a*. [Acridoidea of the U.S.S.R. and adjacent countries. Part I.] [In Russian.] *Opred. Faune SSSR* **38:** 1–378.

—— **&** —— 1951*b*. [Acridoidea of the U.S.S.R. and adjacent countries. Part II.] [In Russian.] *Opred. Faune SSSR* **40:** 1–667.

Berezhkov, R. P. 1956. [*Acrididae of Western Siberia.*] 175 pp. Tomsk. [In Russian.]

Bigalke, R. C. 1968. Evolution of mammals on southern continents, 3. The contemporary mammal fauna of Africa. *Q. Rev. Biol.* **43:** 265–300.

Bolívar, I. 1884. Sur les Orthoptères d'Europe et du bassin de la Méditerranée. *Annls Soc. ent. Belg.* **28:** 102–107.

—— 1887. Especies nuevas ó criticas de Ortópteros. *An. Soc. esp. Hist. nat.* **16:** 89–114.

—— 1889. Ortópteros de Africa del Museo de Lisboa. *Jorn. Sci. math. phys. nat.* (2)**1:** 73–112.

—— 1898. Ortópteros recogidos en Marruecos por D. Jéronimo Olcese. *Actas Soc. esp. Hist. nat.* **27:** 72–78.

—— 1908. Acridiens d'Afrique du Musée Royal d'Histoire naturelle de Belgique. *Mém. Soc. r. ent. Belg.* **16:** 83–126.

—— 1914. Dermapteros y Ortopteros de Marruecos. *Mems R. Soc. esp. Hist. nat.* **8:** 157–238.

Bonnet, E. & Finot, A. 1884–5. Les Orthoptères de la Régence de Tunis. *Revue Sci. nat. Montpellier* (3)**4:** 193–232, 333–365.

Bormans, A. de 1879. *In* Gestro, R., Crociere del violante . . . Appunti sull'entomologia tunisina. *Annali Mus. civ. Stor. nat.* **15:** 405–24.

—— 1884. Le Crociere dell' Yacht Corsaro. VI. Ortotteri. *Annali Mus. civ. Stor. nat.* **20:** 176–181.

—— 1885. Materiali per lo studio della fauna Tunisina raccolti da G. e L. Doria. VII. Orthoptères. *Annali Mus. civ. Stor. nat.* **15:** 405–424.

Box, H. E. 1953. *List of sugar-cane insects.* [v] + 101 pp. London.

Brancsik, K. 1900. Orthoptera e regione Boroma ad fluvium Zambesi. *Jh. naturw. Ver. Trencsiner Kom.* **21–22:** 180–185.

Brunner von Wattenwyl, C. 1882. *Prodromus der europäischen Orthopteren.* 466 pp. Leipzig.

Bünzli, G. H. & Buttiker, W. W. 1956. Insects in S. Rhodesian tobacco culture. Part I. Insects occurring in seed-beds. *Acta trop.* **13:** 352–365.

Burmeister, C. H. C. 1838. *Handbuch der Entomologie.* **2**(2): 591–664. Berlin.

Burr, M. 1898. Orthoptera collected in south-eastern Europe. *Entomologist's Rec. J. Var.* **10:** 267–269, 295–297.

—— 1900. Orthoptera. *In* Peel, C. V. A., On a collection of insects and arachnids made in 1895 and 1897 by Mr C. V. A. Peel, F.Z.S., in Somaliland, with descriptions of new species. *Proc. zool. Soc. Lond.* **1900:** 35–46.

—— 1912. The Orthoptera of Madeira. *Entomologist's Rec. J. Var.* **24:** 29–33.

Butani, D. K. 1961. Annotated list of insects on sugarcane in India. *Indian J. SugCane Res. Dev.* **5:** 126–137.

Butler, A. G. 1881. An account of the zoological collections made during the survey of H.M.S. *Alert* in the Straits of Magellan and on the coast of Patagonia. *Proc. zool. Soc. Lond.* **1881:** 2–140.

Carcasson, R. H. 1964. A preliminary survey of the zoogeography of African butterflies. *E. Afr. Wildl. J.* **2:** 122–157.

Carrick, R. 1959. The food and feeding habits of the straw-necked ibis, *Threskiornis spinicollis* (Jameson), and the white ibis, *T. molucca* (Cuvier), in Australia. *C.S.I.R.O. Wildl. Res.* **4:** 69–92.

Chang, K. S. F. 1939. Some new species of Chinese Acrididae. *Notes Ent. chin.* **6:** 1–59.

Chapin, J. P. 1932. The birds of the Belgian Congo. Part 1. *Bull. Am. Mus. nat. Hist.* **65:** 1–756.

Chapman, R. F. & Robertson, I. A. D. 1958. The egg pods of some tropical African grasshoppers. *J. ent. Soc. sth. Afr.* **21:** 85–112.

Charpentier, T. de 1825. *Horae entomologicae.* 262 pp. Wratislaviae.

Cheke, R. A., Fishpool, L. D. C. & Ritchie, J. M. 1980. An ecological study of the egg-pods of *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae). *J. nat. Hist.* **14:** 363–371.

Cheo, Ming Tsang. 1937. A preliminary list of the insects and arachnids injurious to economic plants in China (cont'd). *Peking nat. Hist. Bull.* **11:** 417–432.

Chesler, J. 1938. Observations on the biology of some South African Acrididae (Orthoptera). *Trans. R. ent. Soc. Lond.* **87:** 313–351.

Chen, F. & Wong, F. 1936. A list of the known fruit insects of China. *Yb. Bur. Ent. Chekiang Prov.* **5**(1935): 82–140.

Chopard, L. 1950. Contribution à l'étude de l'Aïr, Orthopteroïdes. *Mém. Inst. fr. Afr. noire.* **10:** 127–146.

Chopard, L. & Chatterjee, N. C. 1937. Entomological investigations on the spike disease of sandal. (31) Dermaptera and Orthoptera. *Indian Forest Rec.* (Ent.) (N.S.) **3:** 1–30.

Costa, O. G. 1836. *Fauna del regno di Napoli. Ortotteri.* 52 + 16 pp. Naples.

Costantino, G. 1954. La lotta artificiale contro le cavalette mediante prodotti a base di Esaclorocicloesano, di Octacloro di Aldrin e di Eptacloro. *Circol. Oss. reg Fitopatol. Calabria* **13:** 1–10.

Cuthbertson, A. 1934. Biological notes on some Diptera in Southern Rhodesia. *Proc. Trans. Rhod. scient. Ass.* **33:** 32–50.

Davis, D. H. S. 1962. Distribution pattern of southern African Muridae with notes on some of their fossil antecedents. *Ann. Cape prov. Mus.* **2:** 56–76.

De Geer, C. 1773. *Mémoires pour servir à l'histoire des insectes.* **3.** viii + 698 pp. Stockholm.

Del Valle y March, R. G. 1968. Importancia agricola de algumas espécies entomológicas, em Moçambique. *Comunçoes Inst. Invest. agron. Moçamb.* **16:** [3]–148, 1A–27A, 1B–5B, 1C–6C pp.

Descamps, M. 1953. Observations relatives au criquet migrateur africain et à quelques autres espèces d'Acrididae du Nord-Cameroun. *Agron. trop., Nogent.* **8:** 567–613.

—— 1954. Insectes nuisibles aux cultures et insectes prédateurs récemment observés dans le Nord-Cameroun. *Agron. trop., Nogent.* **9:** 174–182.

—— 1972. Geographical regions and taxonomic groups of Acridomorpha in need of study. *In* Hemming, C. F. & Taylor, T. H. C. (Eds), *Proceedings of the International Study Conference on the current and future Problems of Acridology, London, 1970.* xvi + 533 pp. London.

Descamps, M. & Wintrebert, D. 1966. Pyrgomorphidae et Acrididae de Madagascar. Observations biologiques et diagnoses (Orth. Acridoidea) *Eos, Madr.* **42:** 41–263.

Dirsh, V. M. 1953. Morphometrical studies on phases of the desert locust (*Schistocerca gregaria* Forskal). *Anti-Locust Bull.* **16:** 1–34.

—— 1956*a*. Orthoptera. Acridoidea. *In* Hanstrom, B., Brinck, P. & Rudebeck, G. *S. Afr. anim. Life* **3:** 121–272.

—— 1956*b*. The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. *Trans. R. ent. Soc. Lond.* **108:** 223–356.

—— 1957. The spermatheca as a taxonomic character in Acridoidea (Orthoptera). *Proc. R. ent. Soc. Lond.* (A) **32:** 107–114.

—— 1958. Revision of the genus *Eyprepocnemis* Fieber, 1853 (Orthoptera: Acridoidea). *Proc. R. ent. Soc. Lond.* (B) **27:** 33–45.

—— 1961*a*. Review of the genus *Humbe* I. Bolívar 1881 (Acridoidea, Orthoptera). *Ann. Mag. nat. Hist.* (13) **4:** 315–318.

—— 1961*b*. Note on Acridoidea of Africa, Madagascar and Asia. *Eos, Madr.* **37:** 379–398.

—— 1965. *The African genera of Acridoidea.* 579 pp. London.

—— 1966. Acridoidea of Angola. *Publções cult. Co. Diam. Angola* **74:** 11–527.

—— 1975. *Classification of the acridomorphoid insects.* vii + 71 pp. Faringdon.

Distant, W. L. 1892. *A naturalist in the Transvaal.* xvi + 277 pp. London.

Dreux, P. 1961. Recherches écologiques et biogéographiques sur les Orthoptères des Alpes françaises. *Annls Sci. nat.* (Zool.) (12) **3:** 323–766.

Dutt, M. K. 1952. Polyploidy in the spermatocytes of some Acridids. *Proc. 39th Indian Sci. Congr.* **1952:** 312.

—— 1955. On the chromosome complement and meiosis in nine species of Indian grasshoppers. *Proc. zool. Soc., Calcutta* **8:** 111–129.

Dutt, S. C. & Sinha, P. K. 1961. Studies on the life history of the fowl tapeworm *Choanotaenia infundibulum* (Bloch). *Indian J. vet. Sci.* **31:** 121–131.

Dutt, S. C. & Mehra, K. N. 1962. Studies on the life history of *Hymenolepis farciminosa* (Goeze, 1782) (Cestoda: Hymenolepididae). *Parasitology* **52:** 397–400.

Ergene, S. 1954. Homochromer Farbwechsel bei *Oedaleus*-Imagines. *Zool. Anz.* **153:** 110–113.

—— 1955*a*. Weitere Untersuchungen über Farbanpassung bei *Oedaleus decorus. Z. vergl. Physiol.* **37:** 226–229.

—— 1955*b*. Über die Bevorzugung eines homochromen Milieus bei Heuschrecken und Gottesanbeterin. *Zool. Jb.* (Syst.) **83:** 318–323.

—— 1955*c*. [Orthopter erginlerinde homokrom renk degisimi]. Der imaginale homokromer Farbwechsel bei Orthopteren. *Istanb. Üniv. Fen Fak. Mecm.* (B) **20:** 113–116.

—— 1956. Homochromer Farbwechsel bei geblendeten *Oedaleus decorus. Z. vergl. Physiol.* **38:** 311–314.

Fabricius, J. C. 1775. *Systema entomologiae.* [xxxii] + 832 pp. Flensburgi & Lipsiae.

Farabaksh, G. 1961. A checklist of economically important insects . . . in Iran. *Publ. Dep. Pl. Prot. Iran* **1:** 1–153.

Farrow, R. A. 1972. *The African migratory locust in its main outbreak area in the middle Niger: quantitative studies of solitary populations in relation to environmental factors.* **2:** 183–400. Unpublished Ph.D. Thesis, University of Reading.

Fenard, A. 1896. Recherches sur les organes complémentaires internes de l'appareil génital des Orthoptères. *Bull. scient. Fr. Belg.* **29:** 290–533.

Fieber, F. X. 1853. Synopsis der europäischen Orthopteren. *Lotos* **3:** 115–129.

Finot, A. 1895. Faune de l'Algérie et de la Tunisie. Insectes Orthoptères. *Annls Soc. ent. Fr.* **64:** 57–120, 401–552.

—— 1902. Liste des Orthoptères capturés dans le Sahara Algérien par M. le Professeur Lameere. *Annls Soc. ent. Belg.* **46:** 432–435.

Frey-Gessner, E. 1894. Orthoptera gesammelt in der Provinz Oran in Nordafrika von den Herren Prof. Dr A. Forel und Dr L. Zehntrer im Frühjahr 1893. *Mitt. schweiz. ent. Ges.* **9:** 103–109.

Froggatt, W. W. 1903. Locusts and grasshoppers. Part 1. *Agric. Gaz. N.S.W.* **14:** 1102–1110.

—— 1907. The eastern plague locust (*Oedaleus senegalensis* Krauss). Some suggestions how to check them. *Agric. Gaz. N.S.W.* **18:** 539–541.

—— 1910. Locusts in Australia and other countries. *Fmrs' Bull. N.S.W. Dep. Agric.* **29:** 1–40.

Gabriel, B. P. 1968. Entomogenous microorganisms in the Philippines: new and past records. *Philipp. Ent.* **1:** 97–130.

Germar, E. F. 1826. *Fauna insectorum Europae.* **12:** pl. 17. Halae.

Giglio-Tos, E. 1907. Ortotteri Africani. Parte I. *Boll. Musei Zool. Anat. comp. R. Univ. Torino* **22** (554): 1–35.

—— 1923. Missione zoologica del Dr E. Festa in Cirenaica. *Boll. Musei Zool. Anat. comp. R. Univ. Torino* **38** (4): 1–7.

Golding, F. D. 1946. The insect pests of Nigerian crops and stock. *Spec. Bull. Dep. Agric. Nigeria* **4:** 1–48.

—— 1948. The Acrididae (Orthoptera) of Nigeria. *Bull. ent. Res.* **99:** 517–587.

Greathead, D. J. 1963. A review of the insect enemies of Acridoidea (Orthoptera). *Trans. R. ent. Soc. Lond.* **114:** 437–517.

Griffiths, J. F. (Ed.) 1972. *World survey of climatology. 10. Climates of Africa.* xv + 604 pp. Amsterdam.

Hamilton, A. 1976. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. *Palaeoecol. Afr. & surround. Isles & Antarct.* **9:** 63–97.

Harris, W. V. 1949. Record of investigations No. 1.*B*. Section of entomology. General progress report. *Rep. Dep. Agric. Uganda* **1948–1949:** 24–28.

Hemming, C. F. 1966. The vegetation of the northern region of the Somali Republic. *Proc. Linn. Soc. Lond.* **177:** 173–250.

Hollande, A. C. 1926. La signification de l'autohémorrhée des insectes. *Archs Anat. microsc.* **22:** 374–412.

Hollis, D. 1968. A revision of the genus *Aiolopus* Fieber (Orthoptera: Acridoidea). *Bull. Br. Mus. nat. Hist.* (Ent.) **22:** 307–355.

Ikonnikov, N. 1911. Zur Kenntnis der Acridoideen Sibiriens. *Ezheg. zool. Muz.* **16:** 242–270.

Inoue, M. 1972. [Cytological studies on Acrididae. 1. Karyotypes of nine species in the subfamily Oedipodinae.] [In Japanese.] *Kromosomo.* **88–89:** 2785–2794.

Ivanov, E. N. 1934. [On the biology and ecology of *Oedaleus decorus* Germ.] In Lepeshkin, S. N., Zimin, L. S. et al., [*Acrididae of Central Asia.*] 244pp. Tashkent. [In Russian.]

Jacobson, G. G. & Bianchi, V. L. 1902. [*Orthoptera and Pseudo-neuroptera of the Russian Empire and adjoining countries.*] vii + xi + 952 pp. St. Petersburg. [In Russian.]

Jago, N. D. 1963. A revision of the genus *Calliptamus* Serville (Orthoptera: Acrididae). *Bull. Br. Mus. nat. Hist.* (Ent.) **13:** 289–350.

—— 1973. The genesis and nature of tropical forest and savanna grasshopper faunas with special reference to Africa. *In* Meggers, B. J., Ayensu, E. S. & Duckworth, D. (Eds), *Tropical forest ecosystems in Africa and South America: a comparative review.* vii + 350 pp. Washington, D.C.

—— 1977. *Grasshopper survey and control studies: Ethiopia, August 6th to October 6th 1976. Part II.* FAO Unpublished Consultancy Report. 54 pp.

John, B. & Lewis, K. R. 1965. Genetic speciation in the grasshopper *Eyprepocnemis plorans*. *Chromosoma* **16:** 308–344.

Johnsen, P. & Forchhammer, P. 1978. Checklist of the short horned grasshoppers (Acridomorpha) of Rhodesia (Insecta: Orthopteroidea). *Natura jutl.* **20:** 227–236.

Johnston, H. B. 1956. *Annotated catalogue of African grasshoppers.* xxii + 833 pp. London.

—— 1968. *Annotated catalogue of African grasshoppers: supplement.* xiv + 448 pp. London.

Jovancic, L. 1953. Genèse des pigments tégumentaires de la mante religieuse et d'autres animaux, leur rôle biologique et physiologique. *Bull. biol. Fr. Belg.* **87:** 92–104.

Joyce, R. J. V. 1952. The ecology of grasshoppers in east central Sudan. *Anti-Locust Bull.* **11:** 1–99.

—— 1956. Entomological section. *Rep. Minist. Agric. Sudan* **1953–54:** 94–158.

Karsch, F. 1887. Verzeichniss der von Herrn Waldemar Belck 1885 im Damaralande gesammelten Orthopteren. *Ent. Nachr.* **13:** 39–46.

Katiyar, K. N. 1960. Ecology of oviposition and the structure of egg-pods and eggs in some Indian Acrididae. *Rec. Indian Bus.* **55:** 29–68.

Kawamura, K. 1957. Studies on mitotic apparatus and cytokinesis of spermatocytes of nine species of grasshopper. *Cytologia* **22:** 337–346.

Keay, R. W. J. 1959. *Vegetation map of Africa south of the tropic of Cancer.* 24 pp. + 1 map. London.

Kevan, D. K. McE. & Knipper, H. 1955. Zur Systematik, Biologie insbesondere Schwärmbildung, und Morphometrie afrikanischer *Homorocoryphus* (Orth. Tettigon, Conocephalidae). *Veröff. Überseemus. Bremen* (A) **2:** 277–318.

Key, K. H. L. 1930. Preliminary ecological notes on the Acrididae of the Cape Peninsula. *S. Afr. J. Sci.* **27:** 406–413.

—— 1959. The ecology and biogeography of Australian grasshoppers and locusts. Biogeography and ecology in Australia. *Monographiae biol.* **8:** 192–210.

—— 1974. Speciation in the Australian Morabine grasshoppers – taxonomy and ecology. *In* White, M. J. D. (Ed.), *Genetic mechanisms of speciation in insects.* 170 pp. Canberra.

Khan, H. R. & Aziz, S. A. 1974. Influence of different levels of temperature and moisture on the development and hatching of eggs of *Oedaleus abruptus* Thunberg (Orthoptera: Acrididae). *Indian J. Ent.* **35:** 29–31.

—— & —— 1976. Effect of crowding on the hopper developmental period of *Oedaleus abruptus* Thunberg and *Eyprepocnemis alacris alacris* Serville (Orthoptera: Acrididae) under controlled ecological conditions. *Indian J. Ent.* **36:** 142–144.

Kingdon, J. 1971. *East African mammals: an atlas of evolution in Africa,* **1.** 446 pp. London.

Kirby, W. F. 1902*a*. Report on a collection of African Locustidae formed by Mr W. L. Distant, chiefly from Transvaal. *Trans. ent. Soc. London* **1902:** 57–114.

—— 1902*b*. Additional notes on Mr Distant's collection of African Locustidae. *Trans. ent. Soc. London* **1902:** 231–241.

—— 1910. *A synonymic catalogue of the Orthoptera.* **3.** Orthoptera saltatoria. Part II. Locustidae vel Acridiidae. vii + 674 pp. London.

Koch, C. 1960. The Tenebrionidae of southern Africa. 31. Comprehensive notes on the Tenebrionid fauna of the Namib Desert. *Ann. Transv. Mus.* **24:** 61–106.

Krauss, H. A. 1877. Orthopteren vom Senegal gesammelt von Dr Franz Steindachner. *Sber. Akad. Wiss. Wien* (1) **76:** 29–63.

Krauss, H. A. & Vosseler, J. 1896. I. Beiträge zur Orthopterenfauna Orans (West Algerien). *Zool. Jb.* (Syst.) **9:** 515–556.

Latreille, P. A. 1805. *Histoire naturelle générale et particulière des Crustacées et des Insectes.* **Orthoptera, Acrididae. 12.** 424 pp. Paris.

Launois, M. 1979. An ecological model for the study of the grasshopper *Oedaleus senegalensis* in West Africa. *Phil. Trans. R. Soc.* (B) **287:** 345–355.

Launois-Luong, M. H. 1976. Etude de la fecondité d'*Oedaleus senegalensis* (Krauss) dans le Sahel (Région de Maradi) en saison des pluies. G.E.R.D.A.T., P.R.I.F.A.S. Unpublished Report. iii + 15 pp.

La Greca, M. 1970. Considérations sur le peuplement animal terrestre de l'Afrique. *C. R. Somm. Séanc. Soc. Biogéogr.* **409:** 5–33.

Lebrun, J. P. 1971. Quelques phanérogames africaines à aire disjointe. *Mitt. bot. StSamml., Münch.* **10:** 438–448.

Lecoq, M. 1978. Les déplacements par vol à grande distance chez les Acridiens des zones sahélienne et soudanienne en Afrique de l'Ouest. *C. r. hebd. Séanc. Acad. Sci., Paris* **286:** 419–422.

Léonide, J. & Léonide, J.-C. 1969. Contribution à l'étude biologique des Diptères Sarcophagidés parasites d'Acridiens. IV. *Blaesoxipha paolii* Villeneuve. *Bull. Soc. ent. Fr.* **74:** 105–110.

—— & —— 1973. Contribution à l'étude des Diptères Sarcophagides acridophages, VII. Description de *Blaesoxipha dupuisi* n. sp. *Bull. Soc. ent. Fr.* **78:** 277–289.

Léonide, J.-C. 1963. Complément à l'étude de la biologie larvaire de *Symmictus costatus* Loew (Diptera, Nemestrinidae), parasite d'acridiens, et considérations générales sur la biologie des Namestrinidés. *Entomophaga* **8:** 7–33.

Lépiney, J. de & Mimeur, J. M. 1932. Notes d'entomologie agricole et forestière du Maroc, *Mém. Soc. Sci. nat. phys. Maroc* **31:** 1–196.

Libby, J. L. 1968. Insect pests of Nigerian crops. *Res. Bull. agric. Exp. Stn Univ. Wis.* **269:** 1–69.

Linnaeus, C. 1758. *Systema Naturae,* 10th ed. **1.** 824 pp. Holmiae.

Lu, C.-C. 1951–52. Chromosome study in the spermatogenesis of *Oedaleus infernalis. Peking nat. Hist. Bull.* **20:** 117–123.

Mallamaire, A. 1956. Catalogue des principaux insectes, nematodes, myriapodes et acariens nuisibles aux plantes cultivées en Afrique occidentale française et au Togo. *Bull. Prot. Vég.* **1–2** (1955): 23–60.

Manna, G. K. 1954. A study of chromosomes during meiosis in fifteen species of Indian grasshoppers. *Proc. zool. Soc., Calcutta* **7:** 39–58.

Marty, R. 1969. Écologie et biocénotique des Orthoptères des Pyrénées. *Vie Milieu* (C) **20:** 65–169.

McAleer, P. 1977. *Oedaleus senegalensis.* Unpub. report. 20 pp.

Meester, J. 1965. The origins of the southern African mammal fauna. *Zoologica afr.* **1:** 87–95.

Miller, N. C. E. 1929. Acrididae collected in Tanganyika Territory. *Trans. ent. Soc. Lond* **77:** 61–97.

Monod, T. 1971. Remarques sur les symétries floristiques des zones sèches nord et sud en Afrique. *Mitt. bot. StSamml. Münch.* **10:** 375–423.

Morales Agacino, E. 1951. Los ootecas de los Acrididos. *Boln Patol. veg. Ent. agric.* **18:** 89–109.

Moreau, R. E. 1963. Vicissitudes of the African biomes in the late Pleistocene. *Proc. zool. Soc. Lond.* **141:** 395–421.

—— 1966. *The bird faunas of Africa and its islands.* 424 pp. London.

Nagatomi, A. & Iwata, K. 1958. Biology of a Japanese blister beetle, *Epicauta gorhami* Marseul (Coleoptera, Meloidae). *Mushi* **31** (4): 29–46.

Nickerson, B. 1958. Some observations on the Carmine bee-eater *Merops nubicus* Gmelin in the French Sudan. *Ibis* **100:** 454–457.

Nolte, D. J. 1939. A comparative study of seven species of Transvaal Acrididae, with special reference to the chromosome complex. *J. ent. Soc. sth. Afr.* **2:** 196–260.

Norris, M. J. 1959. The influence of daylength on imaginal diapause in the red locust *Nomadacris septemfasciata* (Serville). *Entomologia exp. appl.* **2:** 154–168.

—— 1965*a*. Reproduction of the grasshopper *Aracridium aegyptium* L. in the laboratory. *Proc. R. ent. Soc. Lond.* (A) **40:** 19–29.

—— 1965*b*. The influence of constant and changing photoperiods on imaginal diapause in the red locust. (*Nomadacris septemfasciata* (Serville)). *J. Insect Physiol.* **11:** 1105–1119.

Page, W. W. 1977. Scientific report on a visit to Niger on the Sahel grasshopper project, September 1977. Unpublished Report. 13 pp.

Petagna, V. 1792. *Institutiones entomologicae.* xii + 718 pp. Naples.

Petiver, J. 1702–06. *Gazophylacii naturae et artis decades 1–5 in qua animalia etc.*, pl. 3, fig. 6. London.

Phipps, J. 1959. Studies in East African Acrididae (Orthoptera), with special reference to egg production, habitats and seasonal cycles. *Trans. R. ent. Soc. Lond.* **111:** 27–56.

Plotnikov, V. I. 1921. [Parthenogenesis in Acrididae.] [In Russian.] *Byull. 3go vseross. ént.-fitopatol. Sovêshch.* **7:** 9.

Popov, G. B. 1959. A revision of the genera *Allaga* Karsch and *Sauracris* Burr (Orthoptera: Acrididae). *Trans. R. ent. Soc. Lond.* **111:** 1–26.

—— 1974. The 1974 outbreak of grasshoppers in western Africa. Unpublished Report (OCLALAV 74–10) 9 pp.

Rabaud, E. 1923. Recherches sur la variation chromatique et l'homochromie des arthropodes terrestres. *Bull. biol. Fr. Belg.* **17:** 1–69.

Ragge, D. R. 1955. *The wing-venation of the Orthoptera Saltatoria, with notes on Dictyopteran wing-venation.* vi + 159 pp. London.

Rambur, J. P. 1838. *Faune entomologique de l'Andalousie.* Orthoptera, **2:** 12–94. Paris.

Rattray, J. M. 1960. The grass cover of Africa. *F.A.O. agric. Studies* **49:** i–v, 1–168, 1 map.

Reyneke, A. L. 1941. Notes on some common Karoo grasshoppers. *J. ent. Soc. sth. Afr.* **4:** 197–205.

Risbec, J. 1950. I. La faune entomologique des cultures au Sénégal et au Soudan français. *Trav. Lab. Ent. Sect. soudan. Rech. agron.* **1950:** 1–500.

Risbec, J. & Mallamaire, A. 1949. Les animaux prédateurs et les insectes parasites des riz cultivés en Afrique occidentale. *Agron. trop., Nogent.* **4:** 70–76.

Ritchie, J. M. 1978*a*. Melanism in *Oedaleus senegalensis* and other Oedipodines (Orthoptera, Acrididae). *J. nat. Hist.* **12:** 153–162.

—— 1978*b*. A gynandromorph specimen of *Oedaleus inornatus* Schulthess (Orthoptera: Acrididae). *Acrida* **7:** 149–155.

Roberts, A. 1937*a*. The South African antelopes. *S. Afr. J. Sci.* **33:** 771–787.

—— 1937*b*. The old surviving types of mammals found in the Union. *S. Afr. J. Sci.* **34:** 73–88.

Robertson, I. A. D. 1958. The reproduction of the red locust *Nomadacris septemfasciata* (Serv.) (Orthoptera, Acrididae), in an outbreak area. *Bull. ent. Res.* **49:** 479–496.

Robertson, I. A. D. & Chapman, R. F. 1962. Notes on the biology of some grasshoppers from the Rukwa Valley, S.W. Tanganyika (Orth. Acrididae). *Eos, Madr.* **38:** 51–114.

Roffey, J. 1964. Notes on some locusts and grasshoppers of economic importance in south-east Asia. *Ann. Tech. Bull. Kasetsart ent. phytopath. Soc.* **4:** 74–88.

—— 1965. Report to the government of Thailand on locust and grasshopper control. *FAO Expanded Program of Technical Assistance* no. 2109: 60 pp.

Roy, R. 1962. Le Parc National du Niokolo-Koba (Deuxième Fascicule). VIII. Orthoptera, Acridoidea. *Mém. Inst. fr. Afr. noire* **62:** 109–136.

—— 1965. Contribution à l'étude de la faune de la basse casamance (Sénégal). XIV. Orthoptères Acridoidea. *Bull. Inst. fr. Afr. noire* (A) **27:** 614–631.

—— 1970. Dictyoptères, Chéleutoptères et Orthoptères recueillis par le Dr M. Gaillard à Tambacounda (Sénégal). *Bull. Inst. fr. Afr. noire* (A) **32:** 685–704.

Rungs, C. E. E. 1962. La faune nuisible à la betterave. *Awamia* **3:** 161–174.

Salfi, M. 1925. Contribuzioni alla conoscenza degli Ortotteri libici. 2. Oothecaria e Saltatoria di Cyrenaica. *Bol. Soc. Nat. Napoli* **37:** 90–94.

Saraiva, A. C. 1962. Plague locusts – *Oedaleus senegalensis* (Krauss) and *Schistocerca gregaria* (Forskal) in the Cape Verde Islands. *Estudos agron.* **3:** 61–89.

Saussure, H. de 1884. Prodromus Oedipodiorum, insectorum ex ordine Orthopterorum. *Mém. Soc. Phys. Hist. nat. Genève* **28** (9): 1–256.

—— 1888. Additamenta ad Prodromum Oedipodiorum. *Mém. Soc. Phys. Hist. nat. Genève,* **30** (1): 1–182.

—— 1893. *In* Riley, C. V., Scientific results of the U.S. Eclipse Expedition to West Africa 1889–90. Report on the Insecta, Arachnida and Myriapoda. *Proc. U.S. natn. Mus.* **16:** 579–582.

Schulthess-Schindler, A. de 1898. Orthoptères du pays des Somalis recueillis par L. Robechi-Brichetti en 1891 et par le Prince E. Ruspoli en 1892–93 déterminés et déscrits. *Annali Mus. civ. Stor. nat. Giacomo Doria* (2) **19:** 161–216.

Serville, J. G. A. 1831. Revue méthodique des insectes de l'ordre des Orthoptères. *Annls Sci. nat.* (Zool.) **22:** 262–292.

Shiraki, T. 1910. *Acrididen Japans*. 90 pp. Tokyo.

—— 1952. Catalogue of injurious insects in Japan (exclusive of animal parasites). *Prelim. Study nat. Res. Sect. Supr. Cmmder allied Pwrs* **71** (2): 3–128.

Sjöstedt, Y. 1920. Results of Dr E. Mjöberg's Swedish scientific expedition to Australia 1910–1913, 20. Acridoidea. *Ark. Zool.* **12** (20): 1–66.

—— 1921. Acridoidea Australica. Monographie der bisher von Australien bekannten Heuschrecken mit kurzen Fuhlen. *K. svenska VetensAkad. Handl.* **62** (3): 1–318.

—— 1931*a*. Acrididen aus dem Museum in Canberra. *Ark. Zool.* **22**(A): 1–11.

—— 1931*b*. Acridoidea von der Goldküste, Ob. Volta nebst einer Revision der Gattung *Parga* Walk. *Ark. Zool.* **23** (A) 17: 1–36.

Slifer, E. H. 1939. The internal genitalia of female Acridinae, Oedipodinae and Pauliniinae (Orth: Acrid). *J. Morph.* **65:** 437–469.

Snellen van Vollenhoven, S. C. & de Sélys-Longchamps, E. 1869. *In* Pollen, F. P. L. & Van Dam, D. C., *Recherches sur la faune de Madagascar et de ses Dépendances*. **5** (1). 25 pp. Leyden.

Stal, C. 1873. *Recensio Orthopterorum*. **1.** 154 pp. Stockholm.

Stebaev, I. V. 1957. Orthoptera-fauna in the landscape of the principal watershed in the northern Ergenĭ. [In Russian with English summary.] *Zool. Zh.* **36:** 396–407.

Steck, T. 1915. Orthopteren-Ausbeute aus Tunisien. *Mitt. naturf. Ges. Bern* **1914:** 13–14.

Steinmann, H. 1965. New *Oedaleus* Fieb., and *Bryodema* Fieb. (Orthoptera) species from Central and East Asia. *Annls hist.-nat. Mus. natn. hung.* (Zool.) **57:** 223–228.

Stoll, C. 1813. *Representation exactement colorée . . . des sauterelles etc.* Acrididae. 42 pp. Amsterdam.

Takizawa, S. & Narasawa, T. 1971. Supernumerary chromosomes in two species of grasshopper. [In Japanese with English summary.] *Kromosomo*, **84:** 2679–2683.

Tauber, M. J. & Tauber, C. A. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. *A. Rev. Ent.* **21:** 81–107.

Thunberg, C. P. 1815. Hemipterorum maxillosorum genera illustrata plurimisque novis speciebus ditata ac descripta. *Mém. Acad. Sci. St-Pétersb.* **5:** 211–301.

—— 1824. Grylli monographia illustrata. *Mém. Acad. Sci. St-Pétersb.* **9:** 390–430.

U.S.D.A. 1968. Outbreaks and new records. *Pl. Prot. Bull. FAO* **16:** 92–94.

—— 1976. Hawaii pest report. *Co-op. Pl. Pest Rep. U.S. Dep. Agric.* **1:** 326.

Uvarov, B. P. 1921. A preliminary revision of the genus *Dociostaurus* Fieb. *Bull. ent. Res.* **11:** 397–407.

—— 1922. On some new or little-known South African grasshoppers. *Ann. Mag. nat. Hist.* (9) **9:** 99–113.

—— 1923. Records and descriptions of Orthoptera from north-west Africa. *Novit. zool.* **30:** 51–78.

—— 1925. Notes on the Orthoptera in the British Museum. 4. Identification of types of Acrididae preserved in the Museum. *Trans. ent. Soc. Lond.* **1925:** 265–301.

—— 1926. Grasshoppers (Orthoptera, Acrididae) from northern Nigeria. *Trans. ent. Soc. Lond.* **1925:** 413–453.

—— 1930*a*. Saltatorial Orthoptera collected by Mr. C. L. Collenette in British Somaliland. *Ann. Mag. nat. Hist.* (10) **6:** 176–185.

—— 1930*b*. Synonymic notes on Australian Acrididae. *Ann. Mag. nat. Hist.* (10) **6:** 598–603.

—— 1934. Entomological expedition to Abyssinia 1926–7: Orthoptera of the families Mantidae, Gryllidae, Tettigoniidae and Acrididae. *J. Linn. Soc.* (Zool.) **38:** 591–614.

—— 1936. Studies in the Arabian Orthoptera. I. Descriptions of new genera, species and subspecies. *J. Linn. Soc.* (Zool.) **39:** 531–554.

—— 1941. New African Acrididae. *J. ent. Soc. sth. Afr.* **4:** 47–71.

—— 1942. New Acrididae from India and Burma. *Ann. Mag. nat. Hist.* (11) **9:** 587–607.

—— 1948. Andalusian Orthoptera described by Rambur. *Eos, Madr.* **24:** 369–390.

—— 1977. *Grasshoppers and locusts. A handbook of general acridology.* ix + 613 pp. London.

Van Zinderen Bakker, E. M. 1969*a*. Cold spell of world wide nature at about 5500–4700 BP. *Palaeoecol. Afr. & surround. Isles & Antarct.* **4:** 8.

—— 1969*b*. The southern and south-western Sahara. *Palaeoecol. Afr. & surround. Isles & Antarct.* **4:** 25–28.

—— 1969*c*. The 'arid corridor' between south-western Africa and the Horn of Africa. *Palaeoecol. Afr. & surround. Isles & Antarct.* **4:** 139–140.

—— 1975. The origin and palaeoenvironment of the Namib Desert biome. *J. Biogeogr.* **2:** 65–73.

—— 1976. The evolution of late-quaternary palaeoclimates in southern Africa. *Palaeoecol. Afr. & surround. Isles & Antarct.* **9:** 160–202.

Venkatesh, M. V., Ahluwalia, P. J. S. & Harjai, S. C. 1971. Influence of rainfall on the egg diapause of *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae). *Pl. Prot. Bull., New Delhi* **23** (2): 20–27.

Verdcourt, B. 1969. The arid corridor between the north-east and south-west areas of Africa. *Palaeoecol. Afr. & surround. Isles & Antarct.* **4:** 140–144.

Vosseler, J. 1902*a*. Beiträge zur Faunistik und Biologie der Orthopteren Algeriens und Tunesiens. *Zool. Jb.* (Syst.) **16:** 337–404.

—— 1920*b*. Ueber Anpassung und chemische Vertheidigungsmittel bei nordafrikanischen Orthopteren. *Verh. dt. zool. Ges.* **12:** 108–121.

—— 1920*c*. Beiträge zur Faunistik und Biologie der Orthopteren Algeriens und Tunesiens. II. Theil. *Zool. Jb.* (Syst.) **17:** 1–98.

Walker, F. 1870. *Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum,* Part IV. pp. 605–801. London.

Waloff, N. 1954. The number and development of ovarioles of some Acridoidea (Orthoptera) in relation to climate. *Physiologia comp. Oecol.* **3:** 370–390.

Wells, L. H. 1967. N.E.–S.W. 'Arid Corridor' in Africa. *S. Afr. J. Sci.* **63:** 480–481.

Werner, F. 1914. Ergebnisse einer von Prof. F. Werner im Sommer 1910 . . . Forschungsreise nach Algerien. III. Orthopteren. *Sonderschr. bayer. Akad. Wiss.* (1) **123:** 363–404.

—— 1934. Orthopteren aus dem grossen Atlas von Marokko. *Zool. Anz.* **107:** 3–10.

Whyte, R. O. 1968. *Grasslands of the monsoon.* 325 pp. London.

Winter, B. de 1971. Floristic relationships between the northern and southern arid areas in Africa. *Mitt. bot. StSamml., Münch.* **10:** 424–437.

Winterbottom, J. M. 1967. Climatological implications of avifaunal resemblances between south western Africa and Somaliland. *Palaeoecol. Afr. & surround. Isles & Antarct.* **2:** 77–79.

Zacher, F. 1925. Orthopteren, Geradflügler. *Handb. PflKrank.* (2. Aufl.) **4:** 150–237.

—— 1949. Orthopteroidea, Geradflügler. *Handb. PflKrank.* (5. Aufl.) **4:** 228–352.

Zanon, V. 1924. Contributo alla conoscenza della fauna entomologica della Cirenaica. Ortotteri di Bengasi, *Memorie Accad. pont. Nuovi Lincei* (2) **7:** 229–249.

Zimin, L. S. 1938. Les pontes des acridiens. Morphologie, classification et écologie. [In Russian.] *Opred. Faune SSSR* **23:** 1–83.

Index

Principal references are in **bold**; invalid names are in *italics*.

abruptus 87, 91, 94, 95, **104–107**, 153, 161, 163
amurensis 128–131
arcuatus 84, 99, 101
arenivolans 84, 94, 97
asiaticus 90, 122–124, 126, **127**, 165, 167
australis 84, 87, 90, 94, 95, **101–104**, 153, 165, 166, 168

browni 92, 118–120, **121–122**, 157

caffer 85, 119–121
carvalhoi 88, 89, 93, 95, 101, 114, **116–118**, 135, 144, 153, 156, 163
cephalotes 112, 114, 116
citrinus 84, 151

decorus 84, 85, 88, 90, 92, 93, 96, 101, **122–127**, 130, 153, 161, 162
dilutus 118–121
dimidiatus 94, 97

flavus 84, 88, 91, 92, 95, **149–152**, 153, 157–159
formosanus 87, 91, 93, 96, **132–134**, 153, 167

gracilis 100, 101

inclyta 107, 109
infernalis 84, 87, 91, 94, 96, 122, **128–132**, 133, 153, 163, 167
inornatus 90, 92, 96, **147–148**, 153, 159, 160
instillatus 88, 91, 92, 96, 118, **136–138**, 140, 142, 144, 150, 153, 159, 160, 163, 169, 170
interruptus 85, 88, 90, 93, 95, **134–136**, 153, 156, 157

johnstoni 88, 89, 93, 95, **109–112**, 153, 158, 162

madecassus 107, 109
manjius 128, 130, 131
miniatus 88, 91, 92, 96, **142–145**, 153, 160

mlokoziewiztcki 84, 94, 97, 99
montanus 128, 130, 131

nadiae 91, 92, 96, 144, **145–146**, 153, 159, 160
nigeriensis 88, 89, 93, 95, 111, **112–116**, 117, 118, 122, 153, 156, 163, 165
nigrofasciatus 84, 89, 92, 95, 97, **99–101**, 104, 108, 153, 156, 157

obtusangulus 87, 91, 93, 96, 118, 137, **138–141**, 142, 144, 153, 159, 160, 162

pendulus 90
plana 102–104
plenus 85, 87–89, 93, 95, **118–122**, 150, 152, 153, 156, 157

rosescens 87, 91, 93, 96, 118, 137, 140, **141–142**, 144, 153, 159, 161, 163

senegalensis 84, 85, 87, 89, 92, 93, **94–99**, 100–102, 104, 106, 108, 111, 112, 114, 118, 122, 153, 156, 161, 162, 164, 169, 170
somaliensis 95, 150, **152**, 157, 170

villiersi 138, 140, 141
virgula 90, 93, 95, **107–109**, 153, 163, 166

British Museum (Natural History)
1881–1981

Centenary Publications

Chance, change & challenge

Two multi-author volumes from one of the foremost scientific institutions in the world.

General Editor: P. H. Greenwood

The Evolving Earth

Editor: L. R. M. Cocks

The Evolving Biosphere

Editor: P. L. Forey

In the first volume, *The Evolving Earth,* twenty scientists have been asked to review the present state of knowledge in their particular field, ranging from the origin of the Earth, through ocean sediments and soils to continental drift and palaeogeography.

In the companion volume, *The Evolving Biosphere,* museum scientists have chosen an evolutionary concept—speciation, coevolution, biogeography etc. and related this to the group of animals or plants in which they are specialising. Thus beetles and birds exemplify sympatric and allopatric speciation, butterflies mimicry and certain fishes explosive evolution.

In both volumes the text is supplemented by over one hundred specially-commissioned pieces of two-colour artwork.

These two books will be invaluable to all sixth-form and undergraduate biology and geology students.

The Evolving Earth: 276 × 219 mm, 280pp, 138 line illustrations, 42 halftones

The Evolving Biosphere: 276 × 219 mm, approx. 320pp, 133 line illustrations

Publishing: Spring 1981

Co-published by the British Museum (Natural History), London and Cambridge University Press, Cambridge.

Titles to be published in Volume 42

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. By Michael C. Day.

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. By Barry Bolton.

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). By J. Mark Ritchie.

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). By Angoon Lewvanich.

Printed by The Whitefriars Press Ltd, London and Tonbridge

BM(

BRITISH MUSEUM
GENERAL
2 6 JUN 19
LIBRARY
NATURAL HIST

Bulletin of the British Museum (Natural History)

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae)

Angoon Lewvanich

Entomology series
Vol 42 No 4

25 June 1981

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and are not necessarily completed within one calendar year. Subscriptions may be placed for one or more series. Subscriptions vary according to the contents of the Volume and are based on a forecast list of titles. As each volume nears completion, subscribers are informed of the cost of the next Volume and invited to renew their subscriptions. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Ent.)

© Trustees of the British Museum (Natural History), 1981

ISSN 0524-6431

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Entomology series
Vol 42 No 4 pp 185–298

Issued 25 June 1981

BRITISH M
GENER
2 6 JUN
TURAL H

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae)

Angoon Lewvanich
Entomology and Zoology Division, Department of Agriculture, Bangkhen, Bangkok 9, Thailand

Contents

Synopsis . . . 185
Introduction . . . 185
Material studied . . . 186
Acknowledgements . . . 187
The main characters of Schoenobiinae . . . 188
Taxonomic history of the genus *Scirpophaga* . . . 189
Biology and host-plants . . . 191
Zoogeography of *Scirpophaga* . . . 193
Scirpophaga Treitschke, 1832 . . . 195
  General morphology of *Scirpophaga* . . . 196
  Key to species-groups of *Scirpophaga* . . . 202
  The *praelata*-group . . . 203
    Key to species of the *praelata*-group . . . 204
  The *excerptalis*-group . . . 222
    Key to species of the *excerptalis*-group . . . 222
  The *occidentella*-group . . . 233
    Key to species of the *occidentella*-group . . . 233
  The *lineata*-group . . . 240
    Key to species of the *lineata*-group . . . 240
  The *incertulas*-group . . . 242
    Key to species of the *incertulas*-group . . . 243
  The *gotoi*-group . . . 249
  The *whalleyi*-group . . . 250
References . . . 251
Index . . . 297

Synopsis

The genus *Scirpophaga* is revised. Thirty-five species belonging to seven species-groups are recognized, one genus and twelve species are newly placed in synonymy, *S. excerptalis* is reinstated from synonymy, ten species are transferred to *Scirpophaga*, *S. praelata* var. *xanthopygata* is raised to specific rank, and five species are described as new. One neotype (for *S. virginia*) and nine lectotypes are designated. The main characters of the Schoenobiinae are given and the general morphology of *Scirpophaga* is described; the species are separated mainly on genitalic characters. The zoogeography of the group is briefly discussed and a distribution map of each species is included.

Introduction

The rice and sugar-cane borers of the genus *Scirpophaga* have long been known as species of economic importance. Because of external similarity among the species in this group, the identities of the various species have been very confused. The earlier descriptions are based mainly on external morphology. Except for those of the Australian species, the genitalia have not

Bull. Br. Mus. nat. Hist. (Ent.) **42** (4): 185–298 Issued 25 June 1981

previously been studied. When sexual dimorphism occurs, the male and female have usually been described as two distinct species or even put in separate genera.

The need for taxonomic revision of the species of *Scirpophaga* has become great (Jepson, 1954), many entomologists having experienced considerable difficulty in identifying them. The papers on the systematic position of the species in this group by Butani (1970) and Nagaraja (1972), who tried to establish the stability of the name of the sugar-cane top borer in India, have been unsuccessful since they misidentified the species and wrongly synonymized many names.

The present work consitutes a revision of the taxonomy of *Scirpophaga*. Numerous specimens in the British Museum (Natural History) and on loan from many other museums have been examined. The type-specimens of all species have been studied and dissected. One neotype and nine lectotypes are designated in the interests of nomenclatural stability.

Study of the Old World species of *Scirpophaga* revealed that the specimens in the various collections were badly mixed and showed that, because of numerous misidentifications, the literature could often not be relied upon. In this work many of the taxonomic problems have been clarified. It is hoped that this will be useful not only to taxonomists but also to any entomologist dealing with the control of these stem borers.

The measurements given are those of the wing span. They are calculated by measuring with dividers from the middle of the thorax to the apex of the forewing and mulitplying by two. The measurements are given to the nearest 0.5 mm. The length of the labial palpus was measured in proportion to the length of the compound eye. The latter was measured antero-posteriorly and the former from the basal segment between the eyes to the tip of the scales on the terminal segment. When available, ten specimens were used.

The data of the type-material are fully cited. The localities plotted in the distribution maps are those recorded with the material examined. A dot generally indicates one locality, but may represent several localities when they are very close together.

Material studied

Most of the material studied is in the British Museum (Natural History). Various other museums kindly loaned type- and additional-material. The abbreviations used for the museums or institutions where types and other material are deposited are as follows.

ZM, Amsterdam	Zoölogisch Museum, Amsterdam, Netherlands.
DA, Bangkok	Department of Agriculture, Bangkok, Thailand.
MNHU, Berlin	Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany.
MAK, Bonn	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, West Germany.
UM, Bremen	Übersee Museum, Bremen, West Germany.
ANIC, Canberra	Australian National Insect Collection, C.S.I.R.O., Canberra, Australia.
ZM, Copenhagen	Zoologisk Museum, Copenhagen, Denmark.
IP, Eberswalde	Institut für Pflanzenschutzforschung, Eberswalde, East Germany.
MHN, Geneva	Muséum d'Histoire Naturelle, Geneva, Switzerland.
LN, Karlsruhe	Landessammlungen für Naturkunde, Karlsruhe, West Germany.
RNH, Leiden	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.
BMNH	British Museum (Natural History), London, England.
ZSBS, Munich	Zoologische Sammlung des Bayerischen Staates, Munich, West Germany.
AMNH, New York	American Museum of Natural History, New York, U.S.A.
CNC, Ottawa	Canadian National Collection, Biosystematics Research Institute, Ottawa, Canada.
UM, Oxford	University Museum, Oxford, England.
MNHN, Paris	Muséum National d'Histoire Naturelle, Paris France.
EIHU, Sapporo	Entomological Institute, Hokkaido University, Sapporo, Japan.
NR, Stockholm	Naturhistoriska Riksmuseet, Stockholm, Sweden.
MRAC, Tervuren	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NM, Vienna	Naturhistorisches Museum, Vienna, Austria.
NMNH, Washington	National Museum of Natural History, Washington, D.C., U.S.A.

Approximately 5000 specimens of the genus *Scirpophaga* and other related genera have been studied, and about 1000 genital preparations have been made. The study includes, where it has been possible, examination of the type-specimens of all Asian, African and European species originally described in *Scirpophaga, Schoenobius, Apurima, Topeutis* [*sic*], *Helonastes* and *Niphadoses,* or subsequently placed in these genera.

Acknowledgements

This study was carried out in the Department of Zoology and Applied Entomology, Imperial College of Science and Technology, London. I am deeply grateful to Mr H. E. Goto for supervising the course of this study and for his continuous assistance and encouragement throughout, and to Dr R. G. Davies for advice and clarification of some morphological problems. I am greatly indebted to Professor T. R. E. Southwood, former Head of the Department, for the facilities provided at the college.

Most of the material studied is in the collection of the British Museum (Natural History). I wish to express my sincere thanks to the Trustees of the British Museum (Natural History) and to Dr P. Freeman, Keeper of Entomology, for their permission to study the museum material and for the many facilities provided. I am most grateful to the staff of the Lepidoptera Section for their kind help. My special gratitude is expressed to Dr P. E. S. Whalley for his enthusiastic advice and suggestions concerning the field of investigation and research technique, and also for kindly affording much assistance in securing for study type-material from other museums; to Dr I. W. B. Nye for his help in clarifying some taxonomic and nomenclatural problems and also for generously giving some of his time while visiting continental museums to locate and sort certain type-material essential to this study; to Dr K. S. O. Sattler who provided valuable suggestions, criticism and technical remarks; to Mr M. Shaffer for his enthusiastic help in giving advice, in sorting out from the museum collections the material available for study and in preparing plates for publication; to Mr A. Watson who paid much interest and encouragement in this study, to Mr W. H. T. Tams for his valuable information and suggestions, and to Mr W. G. Tremewan for his help and advice on bibliographic and editorial matters. The photographs of the adult insects were taken in the Museum by Mr P. York. Mr B. Martin also took some of the Stereoscan photographs.

My deep appreciation is also due to Dr J. D. Bradley, Commonwealth Institute of Entomology, London, who paid much interest in this study and gave valuable advice and suggestions. The help from other members of the Commonwealth Institute of Entomology is also acknowledged with thanks.

I wish to express my thanks to the following individuals and authorities for their kind cooperation in making possible the loan of type-specimens and other material, for providing useful information and for the courtesies given when it was possible to visit some of the museums.

Australia: Dr I. F. B. Common, Division of Entomology, C.S.I.R.O., Canberra. Austria: Dr F. Kasy, Naturhistorisches Museum, Vienna. Belgium: Dr L. A. Berger and Dr. P. Basilewsky, Musée Royal de l'Afrique Centrale, Tervuren. Canada: Dr E. G. Munroe and Dr A. Mutuura, Biosystematics Research Institute, Agriculture Canada, Ottawa. Denmark: Dr S. L. Tuxen and the late Dr Niels L. Wolff, Zoologisk Museum, Copenhagen. England: Mr E. Taylor, University Museum, Oxford. France: Dr P. Viette, Muséum National d'Histoire Naturelle, Paris. West Germany: Dr Th. Kruchow, Mrs Szygiarto and Dr H. Hohmann, Übersee Museum, Bremen; Dr U. Roesler, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Dr H. G. Amsel, Landessammlungen für Naturkunde, Karlsruhe; Dr W. Dierl, Zoologische Sammlung des Bayerischen Staates, Munich. Japan: Dr T. Kumata and Dr C. Watanabe, Entomological Institute, Hokkaido University, Sapporo; Dr S. Moriuti, Entomological Laboratory, University of Osaka Prefecture, Sakai. Netherlands: Dr A. Diakonoff, Rijksmuseum van Natuurlijke Historie, Leiden; Mr H. Duffels and Mr W. N. Ellis, Zoölogisch Museum, Amsterdam. Nigeria: Dr G. H. Caswell, Institute for Agricultural Research, Ahmadu

Bello University, Samaru, Kaduna State. Sweden: Mr B. Gustavsson, Naturhistoriska Riksmuseet Stockholm. Switzerland: Dr Cl. Besuchet and Dr B. Hauser, Muséum d'Histoire Naturelle, Geneva. Taiwan: Dr C. B. Chen and Mr Tsong Hong Su, Taiwan Sugar Experiment Station, Tainan. Thailand: Dr M. R. Chakratong Tongyai; Dr Anuwat Wattanapongsiri; Dr R. Syamananda, Mr B. Meksongsee, Mrs V. Nithiuthai, Mrs B. Nanta, Mrs B. Laosinchai and the late Mr P. Pholboon, Department of Agriculture, Bangkok. U.S.A.: Dr J. F. Gates Clarke and Dr K. V. Krombein, Department of Entomology, National Museum of Natural History, Washington.

Dr E. G. Munroe, Biosystematics Research Institute, Agriculture Canada, has given much help during two of his visits to the BMNH.

Finally, I wish to express my sincere thanks to the Colombo Plan Authorities, who made this study possible by providing me with a grant, and to the Thai Government for granting me study leave in the United Kingdom.

The main characters of Schoenobiinae

There is no sharp line separating the Schoenobiinae from the other subfamilies of the Pyralidae. The main characters found in this subfamily are given below and the differences in these characters that occur in some genera are discussed. These are based on an examination of the type-species of most of the described genera in the subfamily.

The Schoenobiinae can be separated from the rest of the Pyralidae by the presence of vein *CuP,* which is developed only at the margin of the forewing (Fig. 6). This vein has been differently homologized by various authors. The character was first mentioned by Forbes (1926), but he called it *1A*. With one exception, all the species of the Schoenobiinae that I have been able to examine have this vein. *Schoenobius pyraustalis* Hampson, described from Argentina, is without vein *CuP,* but the other characters are typical of the Schoenobiinae. The presence of vein *CuP* in the forewing does not, however, automatically place a specimen in the Schoenobiinae. During the course of this work it was found that in *Leechia* South, *Neoschoenobia* Hampson and *Niphopyralis* Hampson, which all possess vein *CuP* and were retained in the Schoenobiinae by Munroe (1956) who referred to the vein as *1A,* lack the other main characters, especially those of the genitalia of this subfamily. Lange (1956: 76) described vein *1A* (*CuP* in the present paper) as being present at the margin of the forewing in the nymphuline tribe Argyractini.

The Schoenobiinae can be divided into two groups according to their wing venation. The first group is characterized by vein R_2 or R_5 or both being anastomosed with R_{3+4} in the forewing. In the second group, veins R_2 and R_3 are free and arise from the cell (Fig. 6).

The proboscis is always reduced. The labial and maxillary palpi are usually porrect, but in *Rupela* Walker the palpi are curved upwards, while in *Acentria* Stephens they are hanging downwards.

The abdomen in the Schoenobiinae is slender. Tympanal organs (Fig. 19) are always present and are situated laterally near the base of the abdomen. In the male, at the postero-median region of the 7th sternite (Fig. 20), there is a large flattened scale-tuft which extends over the 8th sternite (Fig. 21). This membranous area possesses another flattened tuft of shorter scales, the function of which is not known. No trace of a sense organ associated with either of these scale-tufts or with the membranous area of the 8th sternite could be found (Common, 1960). These scale-tufts are very characteristic and are present in most of the genera, though sometimes they are very thin, the exceptions being *Acentria, Calamoschoena* Hampson, *Ramila* Moore and *Tipanaea* Walker. There are at least two species outside the Schoenobiinae, *Endotrichella margaritifera* Hampson in the Pyraustinae and *Parthenodes pallidalis* South in the Nymphulinae, which also have this structure. In females of some schoenobiine genera, there is a tuft of hairs called the 'anal tuft' on the 7th abdominal segment, used for covering the eggs during oviposition.

The genitalia in both sexes (Figs 23-28) provide the most useful diagnostic characters at both the generic and the specific levels. In the male (Figs 23-25), the uncus is usually simple and has the shape of a tapering prong. In *Acentria* and *Calamoschoena* it is simple and plate-like. The gnathos is also simple, but there are some differences: in *Adelpherupa* Hampson and *Promacrochilo* Błeszyński the gnathos is spinose, in *Patissa* Moore, *Argyrostola* Hampson, *Ramila* and some other genera it is slender and armed with teeth on the inner side near the tip, while in some other genera, e.g. *Scirpophaga, Schoenobius* Duponchel, *Catagela* Walker, *Donacaula* Meyrick and *Helonastes* Common, it is slender but without teeth. The articulation of the gnathos with the uncus or partly with the tegumen seems to be of generic significance and is also correlated to the anastomosis of veins R_2 and R_5 with vein R_{3+4} in the forewing. When the gnathos articulates with the uncus, vein R_2 and R_5 are usually free. When it articulates partly with the tegumen, vein R_2 or R_5 or both anastomose with R_{3+4}. The shapes of the dorsal sclerotized thickening of the tegumen were first used by Common (1960) as generic characters, but are considered in this paper as specific differences. The subteguminal processes also provide good taxonomic characters at specific levels. The juxta is usually plate-like, but in *Donacaula* and *Schoenobius* it is broad-based and apically pointed, while in *Catagela* it is long and tapers uniformly from base to apical point.

The presence of coremata in males is also characteristic of the Schoenobiinae. They take the form of plate-like structures with long thread-like scales at their bases. The presence of coremata is correlated with that of a scale-tuft on the 7th abdominal sternite in the male. The four genera in which scale-tufts are absent also lack coremata.

In the female, the elongate, lobe-like, strongly setose papillae anales, together with the long, slender form of both the apophyses anteriores and the apophyses posteriores, are characteristic of the Schoenobiinae. The ostium bursae is usually membranous. The ductus bursae can be either membranous or lined with sclerotized plates. The point of origin of the ductus seminalis is of specific significance. The corpus bursae is membranous or lined inside with spine-like structures when examined by conventional light microscopy, but at very high magnifications (× 1000) it can be seen with the scanning electron microscope that the 'spines' are in fact invaginations of the wall membrane of the corpus bursae. Signa are absent in the subfamily except in *Crambostenia* Swinhoe and *Ramila*.

Genera here transferred from the Schoenobiinae

Erupa Walker	to Crambinae
Gabalaeca Walker	to Crambinae
Leechia South	uncertain subfamily
Lancia Walker	to Crambinae
Neerupa Hampson	to Crambinae
Neoschoenobia Hampson	to Nymphulinae
Niphopyralis Hampson	to Pyraustinae
Schoenerupa Hampson	to Crambinae
Tephroniopsis Amsel	to Tortricidae
Zolca Walker	to Crambinae

Species placed or described in *Scirpophaga* which are here transferred to other genera

Types or paratypes have been examined.

Schoenobius flavus (de Joannis) **comb. n.** VIETNAM: Hanoi.
Tipanaea intactella Walker **comb. rev.** BORNEO: Sarawak.
Patissa melitopis (Meyrick) **comb. n.** ZAIRE.
Patissa nigropunctata (Wileman & South) **comb. n.** TAIWAN.
Patissa percnopsis (Meyrick) **comb. n.** ZAIRE.
Patissa virginea (Zeller) **comb. n.** SOUTH AFRICA: Natal.
Patissa xanthoperas (Hampson) **comb. n.** SUMATRA.

Taxonomic history of the genus *Scirpophaga*

The genus *Scirpophaga* was erected as a monobasic genus by Treitschke in 1832 for the species, *Tinea phantasmatella* Hübner, 1796 (misspelled by Treitschke as *phantasmella*). According to

Treitschke the name *Scirpophaga* is derived from the name of the plant, *Scirpus*, and *phagein*, to eat. The main characters given for the genus are that the hindleg of the adult is long and the pupal stage is white, thin, and transparent, with the hindleg extending beyond the body. Duponchel (1836) added further characters of the genus and at the same time listed four other species as conspecific with *Scirpophaga phantasmella* [*sic*]: *Tinea dubia* Rossi, *Bombyx alba* Hübner, *Phalaena albinella* Cramer and *Eyprepia sericea* Passerini. Among these, *Phalaena albinella* Cramer has subsequently been transferred to *Rupela*, and the last species, *Eyprepia sericea*, cannot be traced from the original reference. In the same volume Duponchel erected one closely related genus, *Schoenobius*.

Zeller (1839) determined *Phalaena Alucita latidactyla* Hübner as conspecific with *Scirpophaga phantasmatella*, but he considered the specific names *phantasmatella* and *latidactyla* to be wrongly latinized, and so he used the name *alba* as the senior synonym.

Walker (1863*a*) wrongly synonymized *Topeutis* (misspelling of *Thopeutis* Hübner, 1818) with *Scirpophaga*. He discovered that *Phalaena praelata* Scopoli, 1763 had priority over *S. alba* and *S. phantasmatella*. At the same time he erected a new monobasic genus, *Apurima*, for the new species *Apurima xanthogastrella*. *Apurima* was subsequently placed as a synonym under *Scirpophaga* by Hampson (1895).

Because of the absence of a clear definition of the genus, the species now in *Scirpophaga* were, in the past, described in various other genera. For example, *excerptalis* and *incertulas* were described in *Chilo*, *innotata* in *Tipanaea*, *occidentella* in *Rupela*. Even in the same species, when sexual dimorphism occurred, the male and female were named as two separate species. Walker (1863*a*) described the male of a species as *Catagela admotella* and later (Walker, 1863*b*), the female as *Tipanaea bipunctifera*. (These two names were subsequently placed as junior synonyms of *Scirpophaga incertulas* (Walker).)

Zeller (1863) redescribed *Scirpophaga* and added six new species to the genus: *cinerea*, *gilviberbis*, *auriflua*, *chrysorrhoa*, *monostigma*, *leucatea*, which with *virginea* Zeller, *albinella* Cramer and the type-species *praelata*, made nine species in all. The present study has shown that only the first five species are true *Scirpophaga*, and that among these only *gilviberbis* is a valid name. In *Schoenobius*, Zeller described the male of *Scirpophaga incertulas* as *minutellus* and the female as *punctellus*. After this, *Scirpophaga* was mentioned in minor detail by many authors, e.g. Heinemann (1865), Moore (1867), Wocke *in* Staudinger (1871), Butler (1880) and Meyrick (1882; 1885; 1889; 1890). The last author (Meyrick, 1889) mentioned that in general *Schoenobius* could be separated from *Scirpophaga* by the relatively long labial palpi, but that in some forms, when there were no differences in length, the rough, erectly spreading tuft in the patagia of the male was a good character for distinguishing *Scirpophaga*. Moore (1886) cited *S. praelata* as type-species of *Scirpophaga*.

Before 1891 the subfamily status of Schoenobiinae had not been recognized and *Scirpophaga* was placed in different families according to various authors. Duponchel ([1846]) erected the family Schoenobidae to include *Scirpophaga* and *Schoenobius*. Walker (1863*a*) placed *Scirpophaga* in the Crambidae. Heinemann (1865) listed this genus under Chilonidae. Moore (1867; 1886) and Butler (1880) placed it under Crambidae. Guenée (1875) erected the family Scirpophagidae to include *Scirpophaga*. Meyrick (1882) placed the genus in the family Schoenobiadae [*sic*] but later (1885; 1886; 1889; 1890) he referred it to Hydrocampidae.

The group, including the three genera *Scirpophaga*, *Schoenobius* and *Donacaula*, was reduced to subfamily status by Ragonot (1891). Hampson (1895) was the first to attempt a classification of the Schoenobiinae. He separated them from the Crambinae by the absence of both the proboscis and a cubital pecten. He recognized 25 genera in the subfamily and, under *Scirpophaga*, listed *Apurima*, *Rupela* and *Tipanaea* as junior synonyms. (The last two were subsequently found to be distinct genera.) Twenty-two species were included in *Scirpophaga* and the synonyms of the species were also listed. This paper caused much confusion to later workers as subsequently it was found that most of the species listed as junior synonyms are actually distinct species, or are synonyms of different species to those under which they were listed. In the following year Hampson (1896) published more or less the same account of the Schoenobiinae as that which appeared in 1895. After this *Scirpophaga* was mentioned by Leech (1901), who studied Chinese, Japanese and Korean material. Rebel *in* Staudinger (1901), studied Palaearctic material, Dyar (1903) North American material and Strand (1918) Taiwan material.

Dyar (1913), in studying the North American species, found that the species that were described under the name *Scirpophaga* in the Nearctic region are not true *Scirpophaga*. For this reason he transferred the North American species to *Rupela*. The genus *Rupela* has been studied in detail by Heinrich (1937).

When Hampson (1919*a*) included *Siga* Hübner [1820] in the subfamily, he changed the name from Schoenobiinae to Siginae because *Siga* had priority. Later in the same year he replaced *Scirpophaga* by *Topeutis* [*sic*] for the same reason, and also described five new species under this genus. Most authors still used *Scirpophaga* as the name of the genus. *Topeutis* [*sic*] remained in the Schoenobiinae for quite a long time. It was only recently that Błeszyński (1965) transferred it to the Crambinae.

In spite of the rejection of the generic name *Topeutis* [*sic*], many authors followed Hampson in changing the name of the subfamily to Siginae. These included Caradja (1925; 1932), de Joannis (1927; 1929) and Marumo (1934). De Joannis (1927) also mentioned species under *Topeutis* [*sic*] but later (1929) changed to *Scirpophaga*.)

Forbes (1923), in studying the Lepidoptera of New York, continued to use Schoenobiinae for the name of the subfamily. Later (1926) he pointed out that the Schoenobiinae could be separated from the other subfamilies by the presence of vein *1A* (*CuP* in the present paper) at the margin of the forewing. He also mentioned that *Siga*, which Hampson (1919*a*) included in Schoenobiinae (resulting in the changing of the name of the subfamily to Siginae), was actually a pyraustine. Shibuya (1928) studied the Schoenobiinae of Taiwan and listed four species in *Scirpophaga: praelata, nivella, excerptalis* and *brunnescens*, and also provided a key to separate these species by using the colour of the forewing and of the anal tuft. Meyrick (1933; 1935) and Turner (1937) placed *Scirpophaga* in the family Schoenobiadae [*sic*].

Munroe (1956), in studying Hampson's Schoenobiinae, supported Forbes (1926) in his opinion that the true Schoenobiinae could be separated from the Crambinae by the presence of vein *1A* at the margin of the forewing. Munroe listed 24 genera, including *Scirpophaga*, in the Schoenobiinae, and also discussed the position of some of the genera removed from the subfamily. This paper has clarified much of our knowledge of the subfamily.

Common (1960), in an important paper, classified the Australian species of *Scirpophaga* and *Schoenobius* by using genital structures. He assigned these species to six genera: *Scirpophaga, Helonastes, Niphadoses* Common, *Catagela, Tryporyza* and *Tipanaea*. Of these, *Helonastes, Niphadoses* and *Tryporyza* were described as new. In *Scirpophaga* he listed eight species, *chrysorrhoa, phaedima, limnochares, xantharrenes, imparella, helodes, percna* and *ochroleuca*. The present study has shown that only *S. phaedima, S. xantharrenes, S. imparella, S. percna* and *S. ochroleuca* are valid species.

Biology and host plants

Biology

The genus *Scirpophaga* contains a group of species whose larvae, so far as is known, are stalk borers of graminaceous crops, including sugar-cane. Some species (e.g. *S. nivella*) have a wide host-range, while others (e.g. *S. incertulas*) are restricted to single host plants. (See list of the host plants of *Scirpophaga*, p. 192.)

The life history of some of the economically important species, especially *S. incertulas* and *S. innotata*, has been studied by many entomologists (Shiraki, 1917; van der Goot, 1925). The female of *S. incertulas* lays eggs in a mass covered with scales from the anal tuft. The eggs are usually deposited on the under surface of the leaf. The number of the egg-masses laid is usually two or three and the number of eggs in each mass between 50 and 60.

The newly hatched larva bores into the stem. In the young plant it destroys the growing point and gives rise to a 'dead heart'. The shoots, except the lowermost two or three, become dry and turn pale yellow or straw-coloured, and come off easily when pulled. Finally, the tiller is killed. In the mature plant the larva bores into the stem above the highest node and disconnects the young panicle, resulting in a 'white head'. In this case the plants may not be killed, but the quality of the ear heads formed on them is drastically affected.

When feeding on young plants the larva moves from plant to plant, but in the mature plant the larva tunnels down to the base of the stem and pupates.

The incubation period is from eight to nine days, the larval period 60 to 66 days and the pupal period nine to twelve days. The entire developmental period is 80 to 85 days, and the moth lives for three to seven days. These periods vary according to the temperature. There are usually five larval instars. The number of generations varies from two to six.

S. incertulas has been claimed to be the most serious pest in the world (Wardle, 1929, cited by Grist & Lever, 1969: 94). In Asia both this species and *S. innotata* are very serious pests of rice, while *S. excerptalis* is a pest on sugar-cane. In Africa, *S. occidentella* and *S. subumbrosa* give rise to many problems in rice pest control. There are also many species of this group which were not previously known to be pests of rice and sugar-cane because of confusion with the species mentioned above.

List of the host plants of *Scirpophaga*

The host plants and countries listed below are taken from the pin-label data of the material examined, or from the references cited.

SPECIES	HOST PLANTS
praelata (Scopoli)	*Scirpus* sp. (Treitschke, 1832; Herrich-Schäffer, 1848); *Scirpus lacustris* (Zeller, 1863; Heinemann, 1865; Rehfous, 1906); *Scirpus validus, Scirpus mucronatus* and *Scirpus littoralis* (Common, 1960, cited under *Scirpophaga limnochares*); *Juncus* sp. (Marumo, 1934).
xanthopygata Schawerda	Unknown.
nivella (Fabricius)	*Oryza sativa* (India, Bangladesh, Thailand, Borneo); *Scirpus* sp. (India); *Cyperus* sp. (India); *Eleocharis* sp. (Hong Kong); *Cladium articulatum* and *Eleocharis dulcis* (Common, 1960, cited under *Scirpophaga chrysorrhoa*).
parvalis (Wileman)	Unknown.
phaedima Common	Unknown.
gilviberbis Zeller	At rest on *Oryza sativa* (Thailand).
percna Common	At rest on *Eleocharis dulcis* (Common, 1960).
imparella (Meyrick)	At rest on *Eleocharis dulcis* (Australia); *Cladium articulatum* and at rest on *Eleocharis sphacelata* (Common, 1960).
xantharrenes Common	At rest on *Eleocharis dulcis* (Common, 1960).
melanoclista Meyrick	Unknown.
excerptalis (Walker)	*Saccharum* sp. (India, Pakistan, Taiwan, Philippines); *Saccharum robustum* (New Guinea); *Saccharum officinarum* (Thailand); *Triticum* sp. (India); at rest on *Oryza sativa* (India).
magnella de Joannis	*Saccharum* sp. (Bangladesh); *Saccharum bengalense* (Pakistan); *Erianthus munja* (India); at rest on *Oryza sativa* (India).
xanthogastrella (Walker)	Unknown.
brunnealis (Hampson)	Unknown.
ochritinctalis (Hampson)	Unknown
bradleyi sp. n.	Unknown.
khasis sp. n.	Unknown.
flavidorsalis (Hampson)	Unknown.
melanostigma (Turner)	Unknown.
tongyaii sp. n.	Unknown.
occidentella (Walker)	*Oryza sativa* (Nigeria).
fusciflua Hampson	*Oryza sativa* (India).
ochroleuca Meyrick	Unknown.
virginia Schultze	*Oryza sativa* (Bangladesh).
subumbrosa Meyrick	*Oryza sativa* (Nigeria, Sierra Leone).
marginepunctella (de Joannis)	Unknown.
serena (Meyrick)	Unknown.

goliath Marion & Viette	Unknown.
lineata (Butler)	*Oryza sativa* (Marumo, 1934).
aurivena (Hampson)	Unknown.
auristrigella (Hampson)	Unknown.
incertulas (Walker)	*Oryza sativa* (Asia).
innotata (Walker)	*Oryza sativa* (Borneo) (van der Goot, 1925; Kapur, 1967); *Saccharum officinarum* (Philippines); *Oryza australiensis* (Common, 1960; Kapur, 1967).
gotoi sp. n.	Unknown.
whalleyi sp. n.	Found in rice fields (India).

Zoogeography of *Scirpophaga*

The genus *Scirpophaga* has a wide distribution in the Old World between the latitude 50°00′N (Bohemia, Czechoslovakia) and 34°53′S (Nowra, Australia). It does not occur in the New World where it is replaced by the genus *Rupela*, the species of which are similar externally to those of *Scirpophaga*. Species from the New World which have been placed in *Scirpophaga* properly belong in *Rupela* or an allied genus.

The normal zoogeographical regions and subregions are used in this paper. The subregions of the eastern part of the Oriental Region follow Gressitt (1956); the rest are mainly after Wallace (1876) with slight modifications. The Indian Subregion includes Sri Lanka in the south and Afghanistan and SW. Iran (Baluchistan) in the north-west.

The distribution patterns of the *Scirpophaga* complex

The Palaearctic Region

There are nine species present in this region. All subregions except the Siberian have representatives of *Scirpophaga*. Two species, *S. parvalis* and *S. gotoi*, are endemic in the Manchurian Subregion.

The distribution pattern of *Scirpophaga* in the Palaearctic Region agrees in general with that of other elements of the Palaearctic insect fauna mentioned by Gressitt (1958), confirming that the insect faunae of Europe and Japan are closely related. This is shown by the distribution of *S. praelata* and *S. xanthopygata*, both of which are present in the European and Manchurian Subregions, but are absent from the Siberian Subregion. It may be surmised that this is because of the deserts and high mountains in the south which form natural geographical barriers. In the Mediterranean Subregion only one species, *S. praelata*, is present.

The Manchurian Subregion is the richest; all nine species are present and two are endemic. The other seven species are shared with the Oriental Region. Japan was connected to the continental mainland in the Pleistocene period (Darlington, 1957) and was finally separated from the continent as a result of tectonic movement of the sea bottom at the end of the Pleistocene (Kostrowicki, 1969). The presence of two endemic species in the Manchurian Subregion, which includes Japan, suggests that Japan is one of the centres of radiation of this group.

The Ethiopian Region

There are eight species known from this region. All are endemic, five of them are in the *occidentella*-group, two in the *excerptalis*-group and one in the *praelata*-group.

The distribution patterns of *Scirpophaga* in the Ethiopian Region follow the distribution of grassland from the west across the continent south-eastwards. In the Malagasy Subregion (Madagascar) five species are found. Of these, one (*S. goliath*) is endemic, and four are shared with the subregions of the mainland. The low percentage of endemism of *Scirpophaga* in Madagascar is quite different from the Thyrididae, in which 27 species out of 30 occurring in Madagascar are endemic (Whalley, 1971). This suggests that most of the species of *Scirpophaga* occurring in Madagascar are probably comparatively recent arrivals.

The Oriental Region

This is the richest of all regions in the number of species of *Scirpophaga*, 22 being recorded of which 10 are endemic. Because this region has a large number of species, the subregions are discussed separately below.

The Indian Subregion. There are nine species in this subregion but only *S. whalleyi* is endemic. This species occurs in both Sri Lanka and India. Since Sri Lanka was presumably connected to India by land late in the Pleistocene period (Darlington, 1957), it is possible that *S. whalleyi* diverged from a closely related species, probably *S. incertulas*, during the interglacial phases which must have been of sufficient duration to allow speciation.

The Indo-Chinese Subregion. This subregion is the richest of all in the Oriental Region. There are 18 species, four of which are endemic. It should be noted that the endemic species occur mainly in the mountain areas of Assam and in the eastern Himalayas. This area is also in the range of distribution of many other species in the genus.

Taiwan has many species in common with the Himalayas and Burma. The similarity of the fauna of Taiwan to that of the Himalayas and Burma was mentioned by Gupta (1962) in his study of the Ichneumonidae. Taiwan also has Palaearctic elements, shown by the presence of *S. praelata* and *S. xanthopygata* which are mainly Palaearctic in distribution. Japan, which is now part of the Manchurian Subregion, was formerly connected with the south China part of the Oriental Region by a land bridge formed by the Ryukyu Islands and Taiwan. When Taiwan was separated, following the submergence which formed the present island chain, a Palaearctic element persisted in the mountains of Taiwan (Gressitt, 1956). This is probably the explanation of the presence of essentially Palaearctic species in Taiwan.

The Malayan Subregion. There are eight species occurring in this subregion, none of them endemic. All of these species except *S. innotata* are also present in the Indo-Chinese Subregion.

The Malayan Subregion includes the Malay Archipelago, Sumatra, Java and Borneo. These areas were once connected together, forming a land mass known as Sundaland. The connection and separation alternated according to the change in sea level during the several glaciations in the Pleistocene period (Zeuner, 1941; 1943). This condition facilitated speciation in various groups of insects in this area, for example some species of Lepidoptera of the subfamily Oretinae (Watson, 1967) and Hymenoptera of the family Ichneumonidae (Gupta, 1962).

Since there are no endemic species of *Scirpophaga* in this subregion, it may be that the species occurring in Sumatra, Java and Borneo are recent arrivals by over-water dispersal or have been introduced inadvertently by man.

The Philippine Subregion. Seven species are found in this subregion. As in the Malayan Subregion, no endemic species are present. All the species occurring here, except *S. xanthogastrella*, are also present in the Malayan Subregion. *S. xanthogastrella* has not been recorded from the Malayan Subregion but this is probably because the area has not been thoroughly collected.

The Celebes Transitional Zone. The seven species occurring in the zone represent a mixture of Oriental and Australian elements. *S. gilviberbis, S. lineata* and *S. incertulas*, which are Oriental species, do not occur further south or east beyond this zone. At the same time *S. percna*, which is an Australian element, does not extend north or west of the Celebes. Because of deep water around the island, Celebes was not connected to the mainland even during the Pleistocene regressions of the sea. The presence of the species of *Scirpophaga* in the Celebes is therefore presumably due to natural dispersal across the water barrier or, perhaps in some cases, to recent introduction.

The Papuan Subregion. This subregion includes New Guinea, the Solomon Islands and the Cape York Peninsula in Australia. Seven species occur in this subregion of which four, *S. nivella*, *S. excerptalis*, *S. flavidorsalis* and *S. melanostigma*, are mainly Oriental, and three, *S. percna, S. ochroleuca* and *S. innotata*, are mainly Australian in distribution.

New Guinea may have had connections with the mainland of Asia via the Malay Archipelago and have been connected to the Cape York Peninsula in north-east Australia during the Miocene-Pliocene tectonic movements (Gressitt, 1956). This would account for the Papuan Subregion having both Oriental and Australian elements.

The Polynesian Subregion. Only one species, *S. nivella*, is known from this subregion and it is found only in New Caledonia and Fiji. It is possible that this species arrived in these islands by natural dispersal across the water or it could have become established following the introduction of rice, which is one of its host plants, into New Caledonia by the French (Grist, 1965).

The Australian Region

The 10 species present in this region all occur on the Australian mainland. No species of *Scirpophaga* occurs in Tasmania or in the New Zealand Subregion.

In Australia the species of *Scirpophaga* occur mainly along the coast in the north and east, probably following the distribution of the tropical grassland.

Three species, *S. phaedima, S. imparella* and *S. xantharrenes*, are endemic. Because of their very similar genitalic structures *S. phaedima* may have evolved from *S. nivella*. *S. percna* and *S. innotata* probably originated in Australia from *S. gilviberbis* and *S. incertulas* respectively, and then spread to the other regions where they are found.

The presence of *S. praelata* in the Australian Region cannot be explained other than by postulating that this species was introduced, probably by the Chinese who came to Australia about 1869 to cultivate rice (Grist, 1965). This view is supported by the morphology of the genitalia, as the specimens of *S. praelata* from Australia have genitalia similar to those from Taiwan but slightly different from those of the European Region.

The distribution of *Scirpophaga* can be summarized as follows.

The Palaearctic Region: 9 species: two endemic, five shared with the Oriental Region, two shared with the Oriental and Australian Regions.

The Ethiopian Region: 8 species, all endemic to the region.

The Oriental Region: 22 species: ten endemic, five shared with the Palaearctic Region, five shared with the Australian Region and two with the Palaearctic and Australian Regions.

The Australian Region: 10 species: three endemic, five shared with the Oriental Region and two shared with the Oriental and Palaearctic Regions.

Of the total of 35 species, 22 occur in the Oriental Region and most are in the Indo-Chinese Subregion (18 species).

Centre of origin and evolution

Since in the Indo-Chinese Subregion, the number of species is greater than in the other subregions, it is possible to speculate that the centre of origin of *Scirpophaga* is in this subregion, especially in the eastern part of the Himalayas and Assam. The probable centre of origin of *Scirpophaga* in the Indo-Chinese Subregion would thus coincide with the place of origin of *Oryza sativa* (Chatterjee, 1951) which is the host plant of many species in this genus. It is doubtful that the pattern of distribution and the diversity of *Scirpophaga* follow the distribution of rice, but there is some coincidental evidence which supports such a possibility. Kratochvil (1956) mentions that the area in which rice can be grown is between 49°00′N in Czechoslovakia and 35°00′S in Australia. This is also more or less the same as the range of distribution of *Scirpophaga* which is between 50°00′N (Bohemia, Czechoslovakia) and 34°53′S (Nowra, Australia).

SCIRPOPHAGA Treitschke, 1832

Scirpophaga Treitschke, 1832: 55; Duponchel, 1836: 8, 16; Zeller, 1839: 170; Guenée, 1845: 334; Duponchel, [1846]: 311; Herrich-Schäffer, 1848: 52; Walker, 1863*a*: 145; Zeller, 1863: 1; Heinemann, 1865: 110; Meyrick, 1882: 151; 1885: 437; Moore, 1886: 387 [*Phalaena praelata* Scopoli designated type-species of *Scirpophaga*]; Meyrick, 1889: 520; 1890: 467; Hampson, 1895: 912; 1896: 45; Rebel, 1901: 11; Leech, 1901: 401; Hampson, 1919*b*: 319 [*Scirpophaga* erroneously cited as a junior synonym of *Topeutis* [*sic*] Hübner, 1818]; Shibuya, 1928: 60; de Joannis, 1929: 607; Marumo, 1934: 13; Jepson, 1954: 20; Common, 1960: 311; Kapur, 1967: 11. Type-species: *Tinea phantasmatella* Hübner, 1796, by monotypy [misspelled *Tinea phantasmella* by Treitschke; junior synonym of *Phalaena praelata* Scopoli, 1763].

Apurima Walker, 1863*a*: 194; Moore, 1886: 388. Type-species: *Apurima xanthogastrella* Walker, 1863, by monotypy. [Synonymized with *Scirpophaga* by Hampson, 1895: 912.]

Tryporyza Common, 1960: 339. Type-species: *Tipanaea innotata* Walker, 1863, by original designation. **Syn. n.**

Scirpophaga is very closely related to the five genera at present recognized in the Schoenobiinae: *Schoenobius, Niphadoses, Helonastes, Catagela,* and *Donacaula*. These genera, except *Donacaula,* have veins R_2 and R_5 of the forewing free, arising from the cell. In the male genitalia, all genera have the gnathos articulating with the uncus. *Scirpophaga* differs from *Schoenobius, Donacaula* and *Catagela* by the last three genera having a pointed juxta, and in *Niphadoses* the gnathos is shorter; in *Helonastes* the female genitalia have the inception of the ductus seminalis close to the corpus bursae. These differences have been noted during the present work, but it was not possible to study these genera in detail. These very small taxonomic differences suggest that further studies are needed to reassess the validity of *Schoenobius, Niphadoses, Helonastes, Catagela* and *Donacaula*.

Common (1960) erected the genus *Tryporyza* and designated *Tipanaea innotata* Walker as type-species. The characters used by him for separating this genus are found mainly in the genitalia. In the male the subteguminal process is curved, hook-like while in the female the ostium bursae is broad, thickened and strongly wrinkled. The present study shows that these characters are of specific significance and not of generic value as mentioned by Common. For this reason *Tryporyza* is placed as a synonym of *Scirpophaga*.

General morphology of *Scirpophaga*

In order to delimit the scope of this investigation, *Scirpophaga* is redefined as a group of Schoenobiinae resembling *Scirpophaga praelata* (Scopoli s. str. and having the following characters in common:

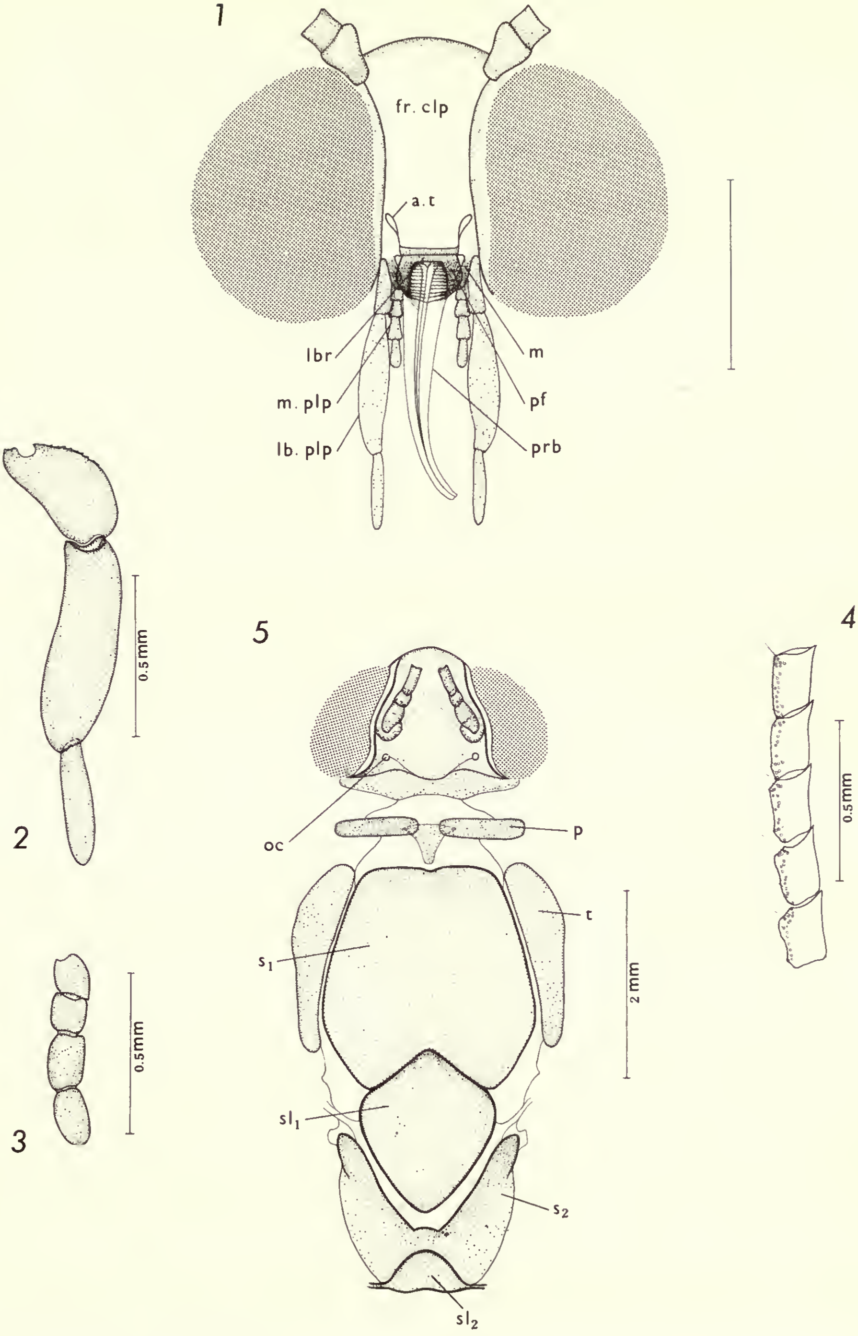
1, in the forewing veins R_2 and R_5 are free and arise from the cell;
2, an abdominal scale-tuft and coremata are present in the male;
3, an anal tuft is present in the female; the corpus bursae is more or less rounded and is usually densely lined with minute spines formed by the invagination of its wall membrane;
4, the juxta in the male is plate-like.

Head (Fig. 1). The general appearance is typical of the Ditrysia. The frons is shallowly rounded. The compound eyes are large, rounded and prominent. One ocellus is present on each side adjacent to the compound eye and posterior to the antenna. The chaetosema, a sensory organ which was first mentioned by Jordan (1923), is a round patch with sensory setae situated on each side near the ocellus. The antennae (Fig. 4) are filiform and weakly serrated. In the male the flagellum is finely ciliate and is approximately three-fifths the length of the forewing; in the female it is thinner and usually much shorter, about one-fifth to half the length of the forewing. The antenna is smooth-scaled dorsally and finely ciliated ventrally, the length of the cilia varying between species and usually shorter in the female.

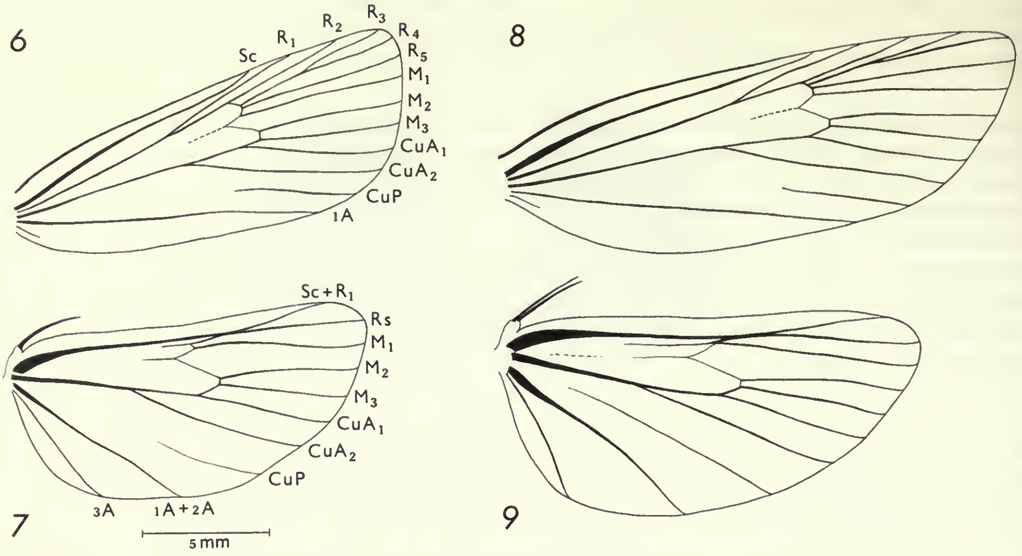
The labrum is a transverse, narrow plate with laterally projecting pilifers. The mandibles are vestigial, attaching to the genae and concealed behind the pilifers. The proboscis is very much reduced. The labial palpus (Fig. 2) and maxillary palpus (Fig. 3) are porrect, the former consisting of three segments, the second of which is the largest. The maxillary palpus is small and short, and consists of four segments whose combined lengths do not exceed half the length of the labial palpus. In the female, the length of both palpi is usually shorter than in the male. The length of the labial palpus varies between species.

Thorax (Fig. 5). The thorax is also typical of the Ditrysia. The patagia are a pair of thin, lobe-like structures on the prothorax. The mesothorax is large and prominent, with a well developed tegula at the base of the forewing. The metathorax is small. No characters of taxonomic value could be found on the thorax.

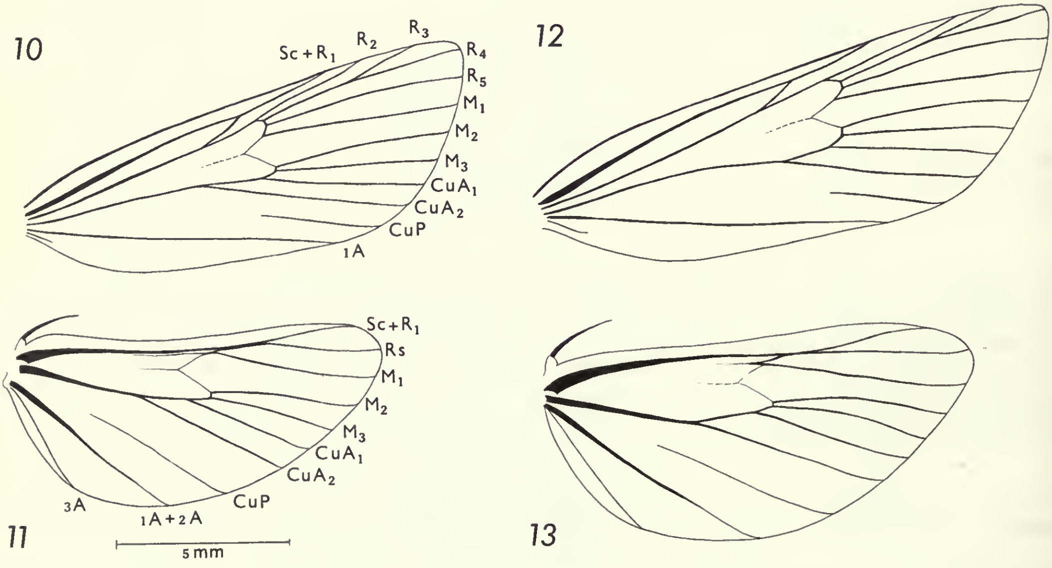
Legs (Figs 16–18). The legs are relatively long. The fore-tibia has a peculiar lamellate spur called the epiphysis at the middle of its inner surface. This spur is regarded as the vestige of an organ formerly developed for cleaning the antennae. The mid-tibia bears a pair of unequal, apical spurs the shorter of which is innermost. The hind-tibia possesses two pairs of spurs, the first situated close to the middle and the second apically. The tarsus consists of five segments, the apical one bearing a pair of claws.


1
fr. clp
a.t
lbr
m. plp
lb. plp
m
pf
prb
2
0.5mm
3
0.5mm
4
0.5mm
5
oc
p
t
s1
2 mm
sl1
s2
sl2

Figs 1–5 Head and thorax of *Scirpophaga praelata* (Scopoli). 1, head (a.t = anterior tentorial pit; fr.clp = fronto-clypeus; lb.plp = labial palp; lbr = labrum; m = mandible; m.plp = maxillary palp; pf = pilifer; prb = proboscis); 2, labial palpus; 3, maxillary palpus; 4, antennal segment; 5, thorax, dorsal view (oc = ocellus; p = patagium; S_1 = mesoscutum; S_2 = metascutum; Sl_1 = mesoscutellum; Sl_2 = postnotum; t = tegula).


6
Sc
R_1
R_2
R_3
R_4
R_5
M_1
M_2
M_3
CuA_1
CuA_2
CuP
1A
8
$Sc+R_1$
Rs
M_1
M_2
M_3
CuA_1
CuA_2
CuP
3A
1A+2A
7
5 mm
9

Figs 6–9 Fore- and hindwing of *Scirpophaga praelata* (Scopoli). 6, 7, male; 8, 9, female.

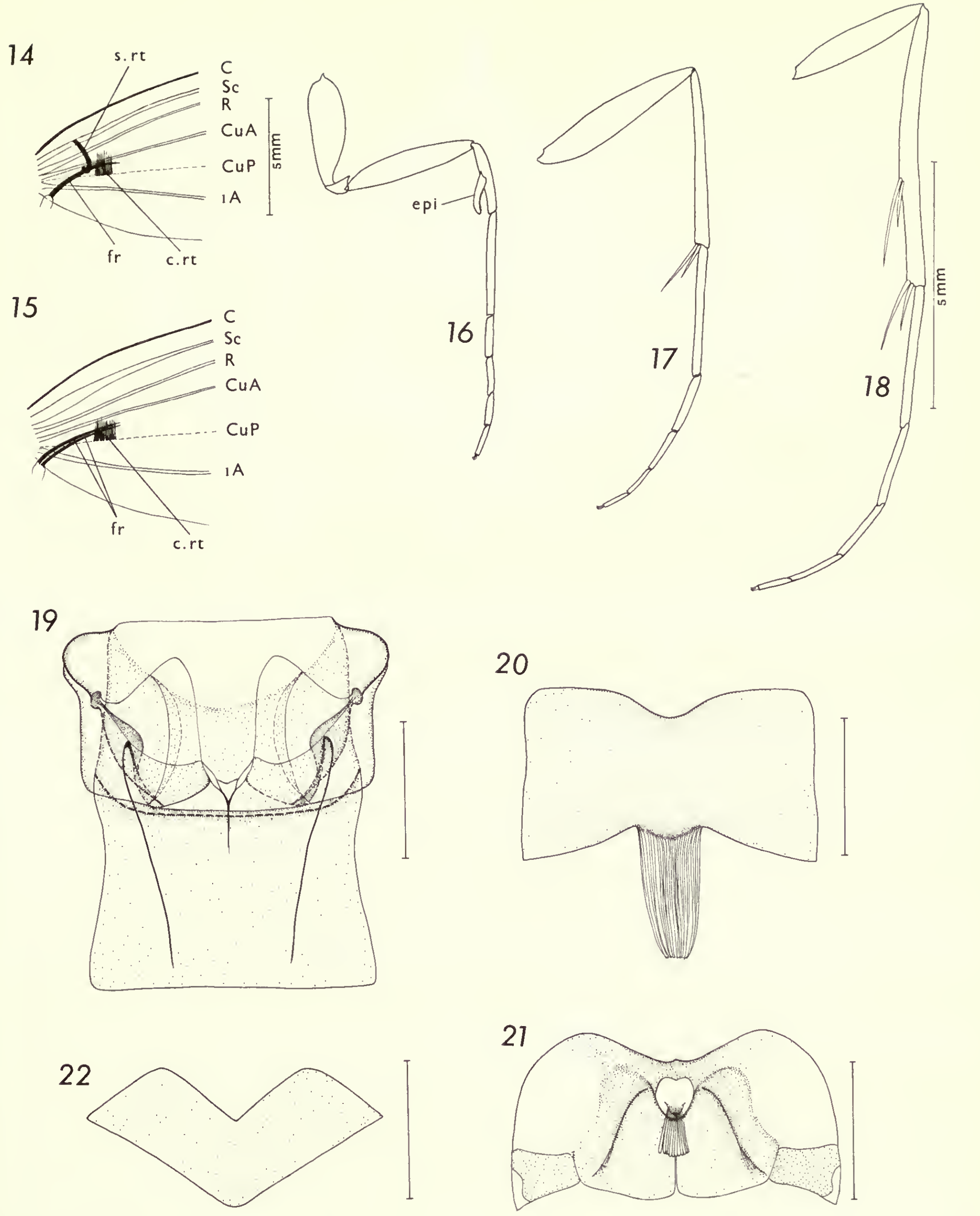

10
$Sc+R_1$
R_2
R_3
R_4
R_5
M_1
M_2
M_3
CuA_1
CuA_2
CuP
1A
12
$Sc+R_1$
Rs
M_1
M_2
M_3
CuA_1
CuA_2
CuP
3A
1A+2A
11
5 mm
13

Figs 10–13 Fore- and hindwing of *Scirpophaga excerptalis* (Walker). 10, 11, male; 12, 13, female.

Wings (Figs 6–15). In the females the apex of the forewing is more pointed than in the males. The colour in general is whitish but there is variation, especially in the males in which the colour varies from pale ochreous white to ochreous. In some species the forewing of the male has markings but in the female it is usually a plain, pale colour.

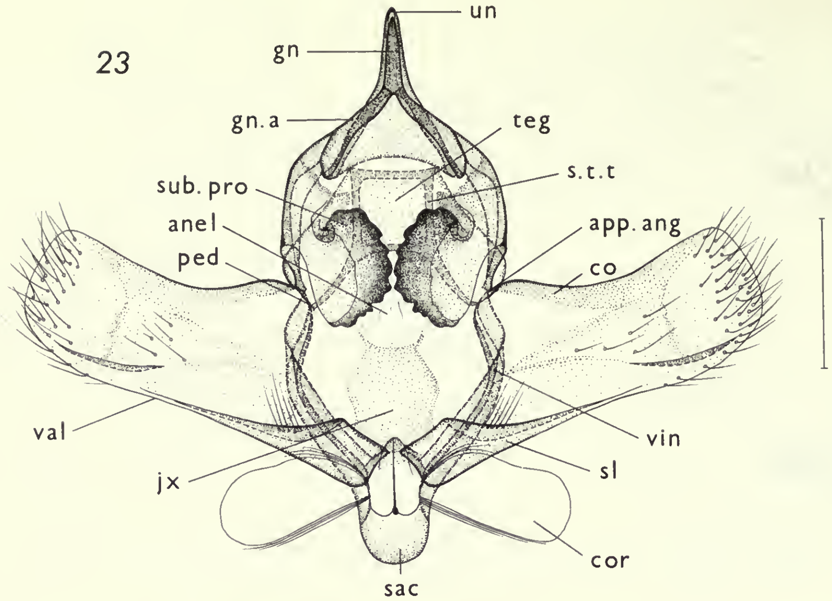
The wing coupling is of the frenate type (Figs 14, 15). A frenulum, subcostal retinaculum and cubital retinaculum are all present in the male, but only the frenulum and cubital retinaculum are found in the female. In the male the frenulum consists of a single bristle, but in the female it may be single or double.

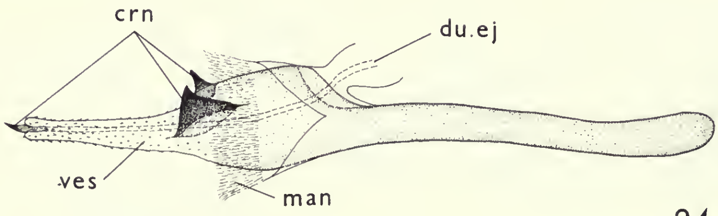
With regard to the wing venation, the terminology used here is that followed by Common (1970). In the


14
s.rt
C
Sc
R
CuA
CuP
1A
5mm
fr
c.rt
15
C
Sc
R
CuA
CuP
1A
fr
c.rt
16
epi
17
18
5mm
19
20
21
22

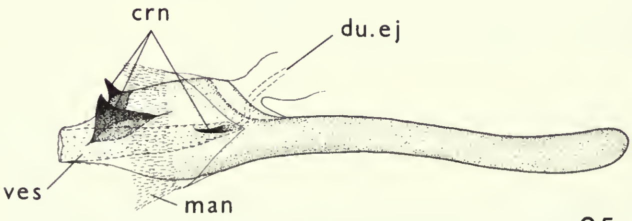
Figs 14–22 *Scirpophaga praelata* (Scopoli). 14, 15, wing-coupling apparatus of (14) male, (15) female. (fr = frenulum; c.rt = cubital retinaculum; s.rt = subcostal retinaculum. 16–18, legs; (16) foreleg (epi = epiphysis), (17) middleleg, (18) hindleg. 19–22, abdominal segments, (19) first abdominal segment, showing tympanal organs, (20) seventh abdominal sternite with scale-tuft, (21) eighth abdominal sternite, (22) eighth abdominal tergite.

23


un
gn
gn.a
teg
s.t.t
sub. pro
anel
ped
app. ang
co
val
vin
sl
jx
cor
sac

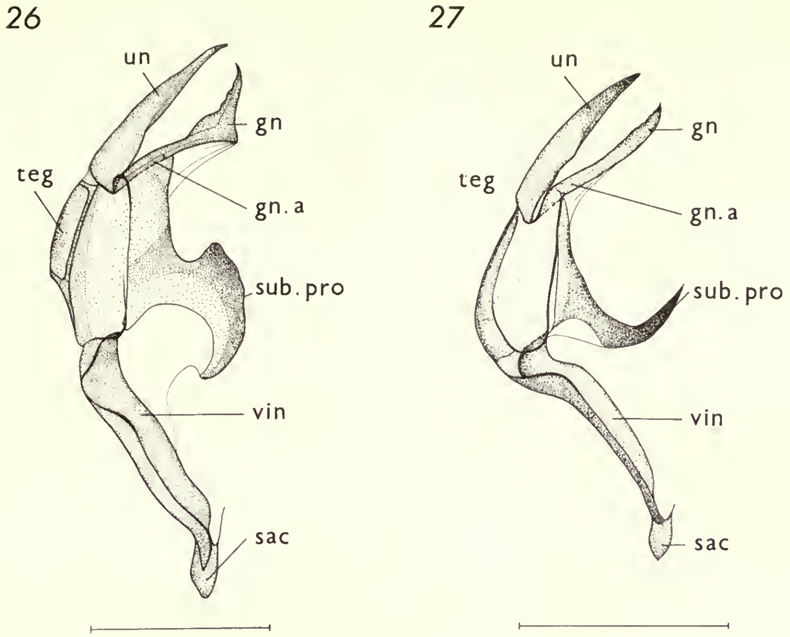

crn
du.ej
ves
man

24


crn
du.ej
ves
man

25

Figs 23–25 Male genitalia of *Scirpophaga praelata* (Scopoli). 23, genitalia, aedeagus removed (anel = anellus; app.ang = appendices angulares; co = costa; cor = coremata; gn = gnathos; gn.a = gnathos arm; jx = juxta; ped = pedunculus; sac = saccus; sl = sacculus; s.t.t = sclerotized thickening of tegumen; sub.pro = subteguminal process; teg = tegumen; un = uncus; val = valva; vin = vinculum). 24, aedeagus, vesica protruded (crn = cornuti; du.ej = ductus ejaculatorius; man = manica; ves = vesica). 25, aedeagus, vesica inside (lettering as in Fig. 24).



Figs 26, 27 Lateral view of male genitalia of *Scirpophaga* species. 26, *S. praelata* (Scopoli), gnathos arms converging abruptly. 27, *S. excerptalis* (Walker), gnathos arms converging gradually. (Lettering as in Fig. 23.)

forewing, whether vein R_1 anastomoses or not with the subcosta is of specific significance. Vein R_2 is free, arising from near upper angle of the cell. Veins R_3 and R_4 are stalked, originating slightly above the upper angle of cell, R_3 at the costa near the apex and R_4 at the apex. Vein R_5 arises from the upper angle of the cell, diverging from R_4 terminally. M_1 approximates to R_5 basally; M_2 originates from above the lower angle of the cell and is more or less parallel to M_1; M_3 arises from the lower angle of the cell. Vein CuA_1 arises from well before the lower angle of the cell; CuA_2 originates at a point two-thirds to three-quarters along the cell. Vein *CuP* is short, developed only at the wing margin; *1A* is complete.

In the hindwing, vein $Sc+R_1$ ends on the costa near the apex, veins R_s and M_1 originate together from the upper angle of the cell, R_s then joins $Sc+R_1$ near the base, terminating on the termen near the apex, M_1 extends to the termen. Vein M_2 arises from above the lower angle of the cell and M_3 from its lower angle close to M_2. CuA_1 arises from before the lower angle of the cell and CuA_2 from about the middle of the cell. *CuP* is obsolete towards the base; *1A+2A* is complete, *3A* is short, straight and complete.

Abdomen (Figs 19–22). In the male, the abdomen is slender and a scale-tuft is present on the 7th abdominal sternite (Fig. 20). In the female an anal tuft is present on the 7th abdominal segment. The colour of the anal tuft is a useful character for distinguishing some of the species.

Genitalia. Male (Figs 23–27). In the male the uncus and gnathos are simple and without any armature. The dorsal sclerotized thickening of the tegumen is of diagnostic importance at the species-group level. In the *praelata*-group it is rectangular, but is somewhat × -shaped in the *excerptalis*- and *occidentella*-groups and more or less triangular in the *incertulas*- and *lineata*-groups. The shape of the subteguminal process is used at the specific level as a taxonomic criterion. It can be of different shapes: plate-like, spine-like or tubercle-like; it is sometimes absent. The anellus is membranous and usually lined with minute spines but in the *occidentella*-group the spines are strongly sclerotized. The manica is lined with spines on the innerside near the aedeagus and is more or less like a broad ring. The arrangement of spines on the manica is sometimes of specific value. The juxta is always simple and in the form of a thin sclerotized plate. The aedeagus is usually elongate and with the cornuti on the vesica of various shapes, mostly spine-like. The valva is simple and not much differentiated but the costa and sacculus are easily seen. The saccus is rounded.

Female (Fig. 28). In the female the genitalia are typical of the Schoenobiinae. The extension of the 8th tergite ventrolaterally and the presence of a group of setae on them are characteristic of the *praelata*-group.

28

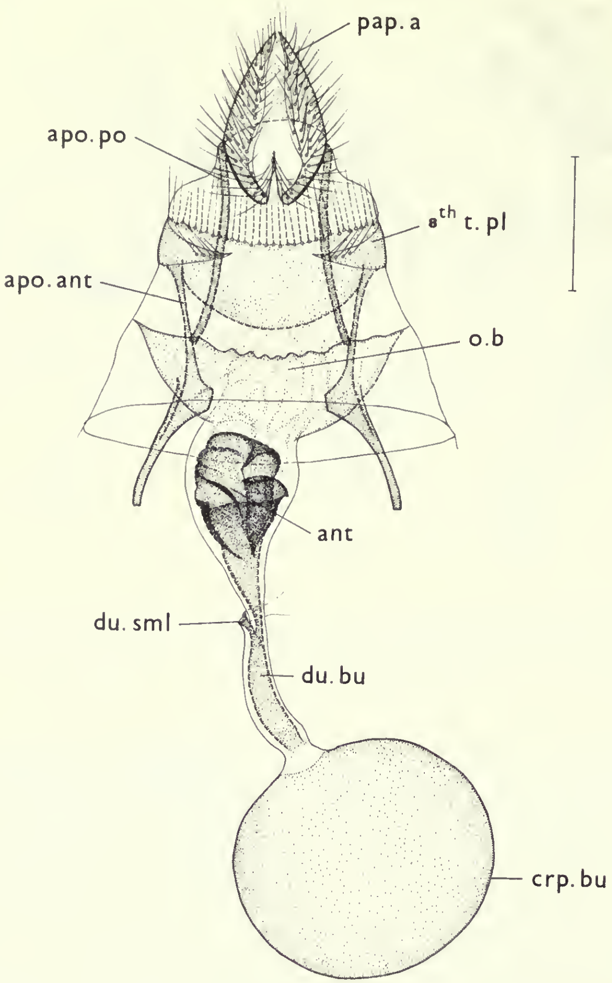


Fig. 28 Female genitalia of *Scirpophaga praelata* (Scopoli) (ant = antrum; apo.ant = apophyses anteriores; apo.po = apophyses posteriores; crp.bu = corpus bursae; du.bu = ductus bursae; du.sml = ductus seminalis; o.b = ostium bursae; pap.a = papillae anales; 8th t.pl = eighth tergal plate).

Key to species-groups of *Scirpophaga*

Males

1 Forewing with vein R_1 anastomosed with *Sc* (Fig. 10) 2
– Forewing with vein R_1 not anastomosed with *Sc* (Fig. 6) 6
2 Subteguminal process membranous, protruded or spine-like, if plate-like, manica with two groups of strong spines 3
– Subteguminal process lobe- or plate-like, manica with uniformly arranged minute spines . 4
3 Subteguminal process membranous, protruded (Fig. 93); dorsal sclerotized thickening of tegumen somewhat triangular; manica with uniformly arranged minute spines.
Aedeagus slender, a group of curved-spined cornuti present (Fig. 94) **whalleyi**-group (**whalleyi**) (p. 250)
– Subteguminal process a strongly sclerotized spine (except plate-like in *S. bradleyi*); dorsal sclerotized thickening of tegumen somewhat × -shaped; manica usually with two groups of strong spines (Fig. 50) . . . . ***excerptalis***-group (p. 222)

4 Anellus lined with strong spines laterally (Fig. 69) **occidentella**-group (p. 233)
– Anellus not lined with strong spines 5
5 Dorsal sclerotized thickening of tegumen ×-shaped; subteguminal process plate-like, broad-based, not strongly sclerotized (Fig. 67) **gotoi**-group (**gotoi**) (p. 249)
– Dorsal sclerotized thickening of tegumen somewhat triangular; subteguminal process plate-like, strongly sclerotized, originating very close to appendices angulares (Fig. 83) **lineata**-group (p. 240)
6 Subteguminal process spine-like.
Dorsal sclerotized thickening of tegumen somewhat triangular; two adjacent unequal curved cornuti present (Figs 90, 92) **incertulas**-group (p. 242)
– Subteguminal process lobe- or plate-like 7
7 Dorsal sclerotized thickening of tegumen rectangular; anellus not lined with strong spines (Fig. 29) **praelata**-group (p. 203)
– Dorsal sclerotized thickening of tegumen ×-shaped; anellus lined with strong spines (Fig. 69) **occidentella**-group (p. 233)

Females

1 Forewing with vein R_1 anastomosed with *Sc* (Fig. 12) 2
– Forewing with vein R_1 not anastomosed with *Sc* (Fig. 8) 6
2 Corpus bursae membranous or with very few spines 3
– Corpus bursae with dense spines 4
3 Ductus seminalis arising from ostium bursae at same level as ductus bursae (Fig. 113) **occidentella**-group (p. 233)
– Ductus seminalis arising from ductus bursae closer to ostium bursae than corpus bursae (Fig. 124) **whalleyi**-group (**whalleyi**) (p. 250)
4 Ductus bursae with sclerotized lining throughout (Fig. 112) **gotoi**-group (**gotoi**) (p. 249)
– Ductus bursae with sclerotized lining only in part, usually membranous 5
5 Papillae anales wrinkled and leathery near tip (Fig. 123) **lineata**-group (p. 240)
– Papillae anales neither wrinkled nor leathery near tip (Fig. 105) **excerptalis**-group (p. 222)
6 Eighth tergal plate produced ventrolaterally with a group of setae; ductus bursae with sclerotized lining throughout (Fig. 95) **praelata**-group (p. 203)
– Eighth tergal plate not produced ventrolaterally; ductus bursae usually membranous 7
7 Ostium bursae strongly wrinkled; corpus bursae usually lined with dense spines in basal three-quarters (Fig. 121) **incertulas**-group (p. 242)
– Ostium bursae not wrinkled; corpus bursae membranous, without spines, with very few spines or densely lined with spines (Figs 113, 117, 118). **occidentella**-group (p. 233)

The *praelata*-group

Forewing with vein R_1 not anastomosing with *Sc*. Frenulum in male a single bristle, in female with single or double bristles.

GENITALIA ♂. Uncus and gnathos moderately long and slender; gnathos arms usually converging abruptly at middle and fused to form a prong with pointed apex; tegumen with dorsal sclerotized thickening rectangular, subteguminal process flattened, plate-like, usually with irregular sinuous margin; manica with dense uniformly arranged minute spines; aedeagus slender, vesica with minute spines, cornuti present.

GENITALIA ♀. Eighth tergal plate produced ventrolaterally with a group of setae on both sides; ostium bursae usually broad, membranous, wrinkled, lined internally with minute spines; ductus bursae with sclerotized lining throughout its length; antrum present in some species; ductus seminalis usually arising at middle of ductus bursae; corpus bursae lined with spines.

The *praelata*-group can be subdivided into two sections by the characters of the females: (1) the *praelata*-section in which a double-bristled frenulum is present and the ductus bursae is provided with an antrum, (2) the *gilviberbis*-section in which the female has a single-bristled frenulum and the ductus bursae is without an antrum. The *praelata*-section includes *S. praelata, S. nivella, S. xanthopygata* and *S. parvalis.* The *gilviberbis*-section contains *S. gilviberbis, S. melanoclista, S. percna, S. imparella* and *S. xantharrenes.* In *S. phaedima,* in which only the male is known, the genitalia are very similar to those of *S. nivella*. There is no doubt that *S. phaedima* is a member of the *praelata*-section.

Key to species of the *praelata*-group

Males

1 Forewing ochreous, usually with markings 2
– Forewing white, pale ochreous white or orange-yellow, without markings 6
2 Gnathos arms converging gradually (Fig. 27); subteguminal process rounded 3
– Gnathos arms converging abruptly (Fig. 26); subteguminal process of various shapes 5
3 Aedeagus with one tridentate and two stout cornuti (Fig. 42) ***gilviberis*** (p. 216)
– Aedeagus without tridentate cornutus, with one or four cornuti 4
4 Aedeagus with one slender cornutus (Fig. 40) ***melanoclista*** (p. 221)
– Aedeagus with four cornuti (one slender and three stout) (Fig. 44) ***percna*** (p. 218)
5 Aedeagus with three cornuti (one slender and two stout) (Fig. 34); subteguminal process usually with strongly sinuous margin (Fig. 33) ***nivella*** (p. 211)
– Aedeagus with four cornuti (one slender and three stout) (Fig. 46); subteguminal process with very fine serrated margin (Fig. 45) ***imparella*** (p. 219)
6 Aedeagus with four cornuti (one slender and three stout) (Fig. 38); subteguminal process rounded (Fig. 37) ***parvalis*** (p. 214)
– Aedeagus with three cornuti (one slender and two stout); subteguminal process of various shapes 7
7 Forewing light orange-yellow; subteguminal process with smooth margin; valva short, truncate (Fig. 47) ***xantharrenes*** (p. 221)
– Forewing white or pale ochreous white; subteguminal process usually with sinuous margin; valva elongate 8
8 Aedeagus with coarse spines on vesica (Fig. 36) ***phaedima*** (p. 215)
– Aedeagus with minute spines on vesica 9
9 Aedeagus strongly swollen in apical third, with one slender and two large stout cornuti (Fig. 30) ***praelata*** (p. 205)
– Aedeagus slightly swollen in apical third, with one slender and two long-based cornuti, larger one usually with bifid tip (Fig. 32) ***xanthopygata*** (p. 209)

Females

The female of *S. phaedima* is unknown.

1 Frenulum double; ductus bursae with antrum (Fig. 95) ***praelata*-section.** 2
– Frenulum single; ductus bursae without antrum (Fig. 101) ***gilviberbis*-section.** 5
2 Antrum with two separated sclerotized plates (Fig. 97), or fused plates to form somewhat hemispherical structure (Fig. 98). ***nivella*** (p. 211)
– Antrum not as above 3
3 Ductus bursae long and slender (Fig. 96) ***xanthopygata*** (p. 209)
– Ductus bursae broad, strongly sclerotized 4
4 Ductus bursae between antrum and ductus seminalis relatively short, slightly evaginated medially (Fig. 99) ***parvalis*** (p. 214)
– Ductus bursae between antrum and ductus seminalis relatively long, not evaginated medially (Fig. 95) ***praelata*** (p. 205)
5 Underside of forewing suffused with fuscous tinge. 6
– Underside of forewing not suffused with fuscous tinge 7
6 Forewing with dark fuscous tinge along costa; ductus bursae with length of sclerotized plate between ostium bursae and ductus seminalis about twice the width (Fig. 104) ***xantharrenes*** (p. 221)
– Forewing without dark fuscous tinge along costa; ductus bursae with length of sclerotized plates between ostium bursae and ductus seminalis about the same as the width (Fig. 103) ***imparella*** (p. 219)
7 Groups of setae always present posterior to ostium bursae; ductus bursae with sclerotized plate between ostium bursae and ductus seminalis long, tube-like, length approximately five times the width (Fig. 100) ***melanoclista*** (p. 221)
– Groups of setae not present posterior to ostium bursae; ductus bursae with length of sclerotized plate between ostium bursae and ductus seminalis less than three times the width 8
8 Ductus bursae with sclerotized plate tapering towards ductus seminalis (Fig. 102). ***perena*** (p. 218)
– Ductus bursae with sclerotized plate tapering towards both ductus seminalis and ostium bursae (Fig. 101) ***gilviberbis*** (p. 216)

Scirpophaga praelata (Scopoli, 1763)
(Figs 29, 30, 95, 125, 126, Map 1)

Phalaena praelata Scopoli, 1763: 198. Syntype(s), YUGOSLAVIA: Carniola [Krain] (probably destroyed, Horn & Kahle, 1936: 252) [not examined].

Tinea dubia Rossi, 1790: 208. Syntype(s), ITALY (no precise locality) (depository unknown) [not examined]. [Synonymized with *praelata* Scopoli by Werneburg, 1864: 254.]

Phalaena Alucita latidactyla Hübner, 1790: 27, pl. 4, fig. U. Syntype(s), ITALY (no precise locality) (depository unknown) [not examined]. [Synonymized with *praelata* Scopoli by Werneburg, 1864: 147.]

Tinea phantasmatella Hübner, 1796: 23, pl. 8, fig. 56. LECTOTYPE ♂, ITALY [Florence (Freyer, 1833)] (*Mazzola*) (NM,Vienna, Type Hb. 56), here designated [examined]. [Synonymized with *praelata* Scopoli by Walker, 1863*a*: 145.]

Topeutis phantasmatalis (Hübner) Hübner, [1825]: 366.

Bombyx alba Hübner, [1828]: pl. 74. figs 309–312; Freyer, 1833: 174, pl. 9, figs 1, 2, pl. 32, fig. 1; Herrich-Schäffer, 1848: 52. Syntype(s), [EUROPE] (depository unknown) [not examined]. [Synonymized with *praelata* Scopoli by Walker, 1863*a*: 145.]

Scirpophaga phantasmella: Treitschke, 1832: 56; 1835: 156; Duponchel, 1836: 18, pl. 267, figs 1a, 1b. [Misspellings.]

Scirpophaga phantasmella var.; Freyer, 1836: 119, pl. 168, figs 1, 2.

Scirpophaga alba (Hübner) Zeller, 1839: 170.

Scirpophaga phantasmella var. *grisea* Guenée, 1845: 334. Syntype(s), YUGOSLAVIA: Carniola [Krain] (depository unknown) [not examined].

Scirpophaga praelata (Scopoli) Walker, 1863*a*: 145; Zeller, 1863: 1; Heinemann, 1865: 110; Wocke, 1871: 216; Butler, 1880: 690; Moore, 1886; 387; Hampson, 1895: 913; Rebel, 1901: 11; Shibuya, 1928: 60 (partim); Marumo, 1934: 2, 15, pl. 1, fig. 3, pl. 2, fig. 7, pl. 3, figs 4, 8, pl. 4, fig. 3; Caradja, 1938*b*: 255; Szent-Ivany & Uhrik-Mészáros, 1942: 130.

Scirpophaga cinerea Zeller, 1863: 1; Heinemann, 1865: 110; Rebel, 1901: 11 (as abnormal form of *praelata* Rebel). Syntype(s), YUGOSLAVIA: Carniola [Krain] (depository unknown) [not examined].

Scirpophaga praelata ab. *cinerea* Zeller; Szent-Ivany & Uhrik-Mészáros, 1942: 130.

Scirpophaga limnochares Common, 1960: 318, figs 4E, 4F, 7C, pl. 1, figs 5, 6. Holotype ♂, AUSTRALIA: N.S.W., Coraki, 10. Jan. 1958 (*I. F. B. Common*) (ANIC, Canberra, genitalia slide no. P. 123) [examined]. **Syn. n.**

♂ (Fig. 125). 26–36 mm. Pale ochreous white. Length of labial palpus approximately 1·2 times diameter of compound eye. Forewing pale ochreous white, underside fuscous; hindwing pale ochreous white, underside suffused with fuscous in costal half.

♀ (Fig. 126). 26–49 mm. White. Fore- and hindwing white on both surfaces; frenulum double-bristled. Anal tuft greyish white.

GENITALIA ♂ (Figs 29, 30). Subteguminal process large, flattened, with irregular sinuous margin; valva elongate, apex rounded; aedeagus strongly swollen in apical third, vesica densely lined with minute spines, one slender and two stout cornuti present.

GENITALIA ♀ (Fig. 95). Ostium bursae broad, membranous; ductus bursae relatively broad, antrum present.

REMARKS. In the original description of *latidactyla*, Hübner (1790) stated that he had specimens from the collections of Kirchmair in Vienna and Gerning in Frankfurt. The figure has the general appearance of *praelata* except that the anal tuft is yellow instead of greyish white as in *praelata*. This yellow anal tuft was commented on by Treitschke (1832), who pointed out that he had never seen it in nature. He doubtfully included *latidactyla* Hübner as a synonym of '*phantasmella*' Hübner (misspelling of *phantasmatella*). Although numerous specimens from western Europe have been examined during this study, I have never seen any with the anal tuft yellow; all have the greyish white anal tuft of *praelata*. There seems no doubt that *latidactyla* Hübner is a synonym of *praelata*, as stated by Werneburg (1864), and that in Hübner's figure the colour of the anal tuft is incorrect.

Werneburg (1864) placed *dubia* Rossi in synonymy under *praelata*. The original description confirms this synonymy, especially in the following characters: '*tota nivea immaculata. . . anus densis pilis albis lanatus in feminis . . . tarsi fusci apice albo annulati*.'

The original published data on *alba* Hübner consist solely of the figures of both sexes, showing both upperside and underside of the wings. The figures of *alba* are identical with *praelata*, and the existing synonymy is confirmed.

The name var. *grisea* was proposed by Guenée for a specimen considered by Freyer (1836) to be a variety of *phantasmella* (misspelling of *phantasmatella*). Freyer examined this moth under the name '*Scirpophaga cinerea* Kokeil', and considered it to be merely an abnormal form of *phantasmella* [*sic*]. Freyer mentioned that, although there was a difference in the colour of the forewing, it had the same mode of life and habitat.

Zeller based his description of *cinerea* on Freyer's figure (Freyer, 1836: pl. 168, figs 1, 2) and considered it as a distinct species. It was treated as an abnormal form of *praelata* by Rebel (1901) and Szent-Ivany & Uhrik-Mészáros (1942).

In the male of *S. praelata*, individual variation is found in the coloration of the forewing. The colour varies from pale ochreous white to pale ochreous. Two specimens from Japan have pale greyish ochreous forewings. In the male genitalia there is some individual variation in the length of the uncus and gnathos and in the depth of the sinuations in the margin of the subteguminal process. The coloration in the female is constant.

In the extensive material examined of this species, most of the specimens from the Mediterranean Subregion (Syria, Lebanon and Turkey) were found in both sexes to be smaller than specimens from other regions. Female specimens from the Manchurian Subregion and Taiwan have the forewing more pointed and the anal tuft shorter and less dense than in specimens from the European Subregion. The genitalia also show slight differences. All six available male specimens from the Mediterranean Subregion have the subteguminal process pointed posteriorly, while the only available specimen from Iran has a more or less rounded subteguminal process as in European specimens. No differences in the genitalia could be found in the three available male specimens from Japan when these were compared with European specimens. Three male specimens from Taiwan have the subteguminal process pointed posteriorly and with a narrower sclerotized band in the margin than in the European specimens, while the fourth specimen is intermediate, rounded but with a narrower sclerotized band in the margin of the subteguminal process. In the female genitalia, specimens from the Manchurian Subregion and Taiwan have the ductus bursae slightly shorter than those from the European Subregion. No differences could be found between female specimens from the Mediterranean and European Subregions. More male specimens from the Asiatic region need to be examined before a decision can be reached regarding any subspecific status.

The Australian specimens which Common (1960) described as *Scirpophaga limnochares* have greyish ochreous forewings in the males. In the genitalia, the subteguminal process is slightly pointed posteriorly and the sclerotized band at the margin is narrow as in the specimens from Taiwan. No difference could be found in the female, except that the ductus bursae of Australian specimens is slightly longer than in those from Taiwan. It is probable that the Australian specimens were introduced from Taiwan or Japan.

This species is the only representative of the *Scirpophaga* complex found in the European and Mediterranean Subregions. In western Asia it can only be confused with *S. xanthopygata* but in China, Japan and Taiwan it has been confused with many species. The genitalia, especially the shape of the cornuti in the male and the broad ductus bursae in the female, are characteristic in this species.

BIOLOGY (for host plants see p. 192). A brief account of the life history of *Scirpophaga praelata* has been given by Treitschke (1832) and a more complete one by Rehfous (1906). The two accounts do not agree in some respects. Treitschke stated that the newly hatched larva first bored into the upper part of the stem of the sedge, then tunnelled downwards and formed a cavity in the root. It then ascended within the stem and made a hole in the wall of the latter above the water level. The hole was covered with a thin membrane and served as an exit for the imago. Pupation took place in the stem below the water level. The chamber where it pupated was about 4 cm long. The larva, pupa and adult were present at the same time. Thus, according to Treitschke, the life history of this species involves only one stem of the plant and there is more than one generation in a year.

However, from the study of Rehfous, it appears that there is only one generation a year and the life history involves two stems of *Scirpus lacustris,* one in winter and the other in spring. He observed that the males were attracted to light but the females could only be caught on the host plants. Mating and oviposition took place at night. The eggs were laid in a mass on the stem of the food plant about 60–70 cm above water level and were covered with a layer of scales from the anal tuft of the females. The egg was soft, elongate, translucent and yellowish, measuring 0·75 × 0·25 × 0·25 mm.

Hatching began 15 days after oviposition. The newly hatched larva bored into the stem and tunnelled to the root. It took about 15 days to reach the root where it stopped feeding and passed the winter from the end of August. When the hibernation chamber was completed, the larva closed the top with impermeable silk to prevent water penetrating when the aerial stem died and was carried away by the current. In the hibernation chamber the larva underwent the second moult.

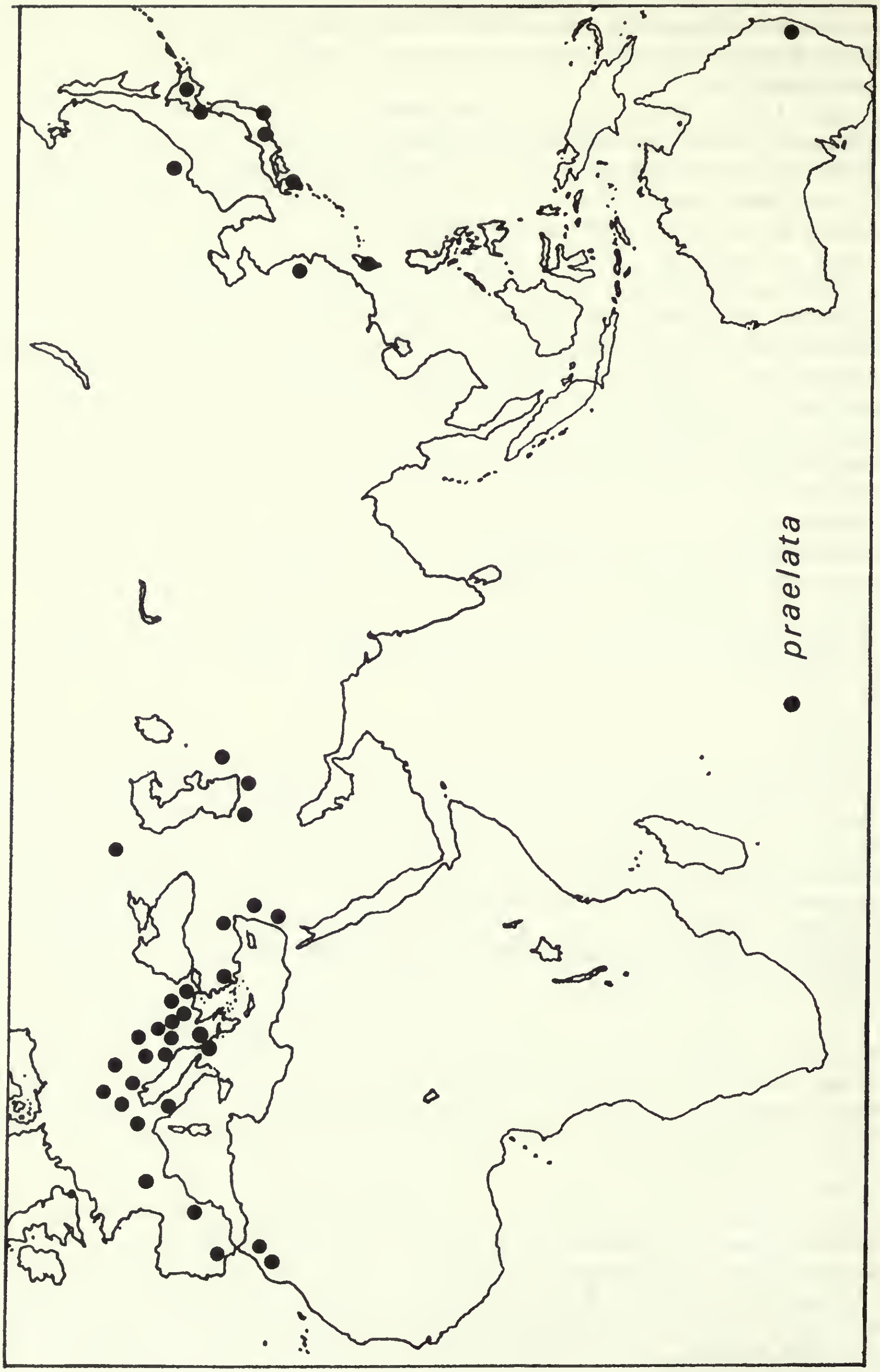
In spring, towards the end of April, when the stems were sprouting, the larva left the hibernation chamber and bored into a new stem, where it tunnelled down to the root; during this time it moulted for the third time. After reaching the root the full-grown larva tunnelled up again for a variable distance to make an exit for the adult, usually below the water level. The pupal chamber was 2 cm long and situated about 3–4 cm below the exit hole, and both ends were covered with an impermeable substance. The adult emerged from the hole under the water, passed through the water and climbed up the stem. It was noticed that in the spring there was only one larva per stem, while in winter there were usually three or four larvae and sometimes as many as nine.

Although Rehfous did not mention how long it took to complete the life cycle, his observation that the larva overwintered suggests that there was only one generation in a year.

DISTRIBUTION. Japan, Taiwan, China, U.S.S.R., Iran, Syria, Lebanon, Turkey, Greece, Bulgaria, Rumania, Czechoslovakia, Hungary, Yugoslavia, Austria, Italy, France, Spain, Morocco, Algeria, Australia.

MATERIAL EXAMINED

Japan: 1 ♀, Hakodate, viii.1866 (*Leech*) (BMNH); 1 ♀, Hakodate (BMNH); 1 ♀, Hokkaido, Kamuikotan, 17.vii.1952 (*Mutuura*) (CNC, Ottawa); 1 ♂, 1 ♀, Junsai Numa, Oshima, Hokkaido, 25, 29.vii.1896, 1902 (*Wileman*) (BMNH); 1 ♂, Amamiosima, Santarotoge, Kyushu, 28.iv.1960 (*Kodama*) (CNC, Ottawa); 1 ♂, Amami, Shinmura, 28.iv.1960 (*Mutuura*) (CNC, Ottawa); 13 ♀, Hamamatsu, Honshiu, 13.vi.1963 (*Mutuura*) (CNC, Ottawa); 1 ♀, Yokohama, 16.viii.1911 (*Höne*) (MAK, Bonn). **Taiwan**: 14 ♀, Anping, vii.–26.ix.1905 (*Wileman*) (BMNH); 1 ♀, Kanshirei, iv.1909 (BMNH); 1 ♂, Takow, 16.viii.1904 (*Wileman*) (BMNH); 3 ♂, 10 ♀, Tainan, vi.–xi.1904,1905,1906 (*Wileman*) (BMNH); 1 ♀, no further data (BMNH). **China**: 1 ♀, Hsü-Chia-Hui (Zi Kaweg) (MNHN, Paris). **U.S.S.R.**: 1 ♀, Ussuri, Nicolsk, vii.1912 (*Moltrecht*) (BMNH); 1 ♀, 1916 (*Dworzak*) (NM, Vienna); 1 ♀, Ussuri Railway, Chabarovsk, 22.vi.1910 (*Borsow*) (BMNH); 1 ♀, Ussuri, 1913 (*Moltrecht*) (BMNH); 1 ♂, 1 ♀, Sarepta (BMNH); 1 ♂, 1 ♀, Geok-tepe, iv.1903 (LN, Karlsruhe); 2 ♀, Geok-tepe, 23.v.1903 (MNHN, Paris). **Iran**: 1 ♂, 1 ♀, South Caspian, Shahi, 19–26.viii.1961 (*Sutton*) (BMNH); 1 ♀, Enzeli, 19.vi.1919 (*Buxton*) (BMNH). **Syria**: 1 ♀, Tartus, 16.vi.1950 (LN, Karlsruhe); 2 ♂, 1 ♀, no further data (MNHN, Paris). **Lebanon**: 1 ♂, 6 ♀, Beirut (BMNH). **Turkey**: 2 ♂, 2 ♀, Amanus S., Yüksek Dagh, viii.1931, 1–15.v.1932 (ZSBS, Munich); 1 ♂, Kusadasi, 22.vii–11.viii.1967 (*Roesler*) (MAK, Bonn); 2 ♂ [unreadable data] (MAK, Bonn); 1 ♀, Adana, Anatolia, 3–12.vi.1934 (BMNH). **Greece**: 1 ♀, Kerkira (Corfu), 8.vii.1902 (BMNH); 1 ♂, Macedonia, Ochrid, 12–24.vi.1939 (*Lunak*) (NM, Vienna); 1 ♂, 1 ♀, Macedonia, Ochrid, 27.vi.1954 (*Thurner*) (ZSBS, Munich); 2 ♂, 5 ♀, Macedonia, 29.v.–2.vii.1918 (*Wolley-Dod*) (BMNH). **Bulgaria**: 1 ♂, 1 ♀, Sistov, 10–20.vii.1933 (ZSBS, Munich). **Rumania**: 1 ♀, Bucarest (*Montandon*) (MNHN, Paris); 1 ♀, Treskovac, nr Szvinicza, Krosso Szeroeny C., 26.vii.1912 (BMNH); 1 ♂, Szvinicza, Krosso Szeroeny C., 13.vii.1912 (BMNH); 1 ♀, Varniseo, nr Szvinicza, Krosso Szeroeny C., 580 m, 3.vii.1962 (BMNH). **Czechoslovakia**: 1 ♂, 1 ♀, Bohemia, 15.vii.1912 (ZM, Amsterdam). **Hungary**: 2 ♀, Budapest, 18.vii., 2.viii.1898 (BMNH); 1 ♂, 1 ♀, Budapest (ZSBS, Munich); 1 ♂, 4 ♀, Nagy Ngir nr Kecskemet, 7.vi.–30.vii.1915 (*Predota*) (BMNH); 3 ♀, Szikra nr Kecskemet, 14.vii.1914 (*Predota*) (BMNH); 2 ♀, Nyirbator, 5.vii.1915 (*Predota*) (BMNH); 1 ♂, 5 ♀, Hortobagy, Hajdu C., 8–14.vii.1912 (*Predota*) (BMNH); 2 ♂, 4 ♀, P. Peszer, Pest C., 8–18.vi.1911 (BMNH); 6 ♂, 3 ♀, 20–23.vi.1913 (BMNH); 1 ♂, 1 ♀, Peszer, Turgan, 10.vii.1928 (*Daniel*) (ZSBS, Munich); 5 ♀, Flamunda, Deliblat, 16–25.vi.1909,1911 (BMNH); 1 ♂, Erkeseru Bihar C., 18.vii.1912 (BMNH); 1 ♀, Csehtelek, Bihar C., 27.vii.1911 (BMNH). **Yugoslavia**: 10 ♂, 24 ♀, Slavonien, Kupinovo, 24.vi.–1.viii.1913



Map 1

(*Predota*) (BMNH); 3 ♂, 3 ♀, Slavonien, Assanjo, 22–28.vi.1913 (*Predota*) (BMNH); 2 ♂, 3 ♀, Slavonien, Obrez, 19.vi.–29.vii.1913 (*Predota*) (BMNH); 1 ♀, Pokostane, 20.vi.1965 (ZSBS, Munich); 1 ♀, Fiume (Rijeka) (*Krauss*) (NM, Vienna); 5 ♂, 3 ♀, Drava Sarvas, Szerem C., 6.vii.–20.viii.1909 (BMNH). **Austria**: 1 ♂, 2 ♀, Hansag Umg., 29.vi.–7.viii.1921 (*Predota*) (BMNH); 1 ♀, Burgenland, Hansag, 26.vi.1954 (*Kasy*) (NM, Vienna); 1 ♀, Gramatneusiedl, Fürbachwiesen, 18.vii.1960 (*Kasy*) (NM, Vienna); 1 ♀, Graz, 22.vii.1917 (ZSBS, Munich); 1 ♀, Graz-Styria, 4.vii.1904 (ZM, Amsterdam); 1 ♂, 1 ♀, Marchfeld, vii.1939 (*Lunak*) (NM, Vienna); 1 ♂, 1 ♀, Prater, iii.1876 (BMNH); 2 ♂, 1 ♀, Prater, xii.1881 (BMNH); 1 ♀, Burgenland, Zitzmannsdorfer Wiesen, 28.vii.1956 (*Kasy*) (NM, Vienna); 1 ♀, Burgenland, Zitzmannsdorfer Wiesen (*Reisser*) (LN, Karlsruhe). **Italy**: 1 ♂, Le Sarche, vii.1897 (*Rebel*) (NM, Vienna). **France**: 1 ♂, Feurs, vii.1909 (BMNH). **Spain**: 2 ♀, Valencia, 10–11.vi.1960 (*Sattler*) (ZSBS, Munich); 1 ♀, Andal, Huelva, El Rocio, 15.iv.1938 (*Marten*) (NM, Vienna). **Morocco**: 2 ♂, Rabat, 1914 (*Théry*) (BMNH). **Algeria**: 1 ♀, Sebdou, iv.1913 (*Théry*) (BMNH). **Australia**: 1 ♂, 2 ♀ (allotype and paratypes of *Scirpophaga limnochares* Common), N.S.W., Coraki, at rest on *Scirpus validus*, 12.iii.1958 (*Common*) (ANIC, Canberra).

Scirpophaga xanthopygata Schawerda, 1922 **stat. n.**

(Figs 31, 32, 96, 127, 128, Map 2)

[*Scirpophaga excerptalis* Walker sensu Leech, 1901: 402 (partim). Misidentification]

Scirpophaga praelata var. *xanthopygata* Schawerda, 1922: 11; Caradja, 1938*a*: 91. LECTOTYPE ♀, U.S.S.R: 'Nikolsk Ussurijsk, ab. *xanthopygata* Schaw. Type 3' (UM, Bremen), here designated [examined].

♂ (Fig. 127). 22–41 mm. Pale ochreous white. Length of labial palpus approximately 1·2 times diameter of compound eye. Forewing pale ochreous white, underside fuscous; hindwing pale ochreous white, underside suffused with fuscous in costal half.

♀ (Fig. 128). 23–47 mm. White. Fore- and hindwing white on both surfaces, sometimes upperside of forewing suffused with very pale ochreous white; frenulum double-bristled. Anal tuft pale ochreous yellow.

GENITALIA ♂ (Figs 31, 32). Subteguminal process large, flattened, with sinuous margin; aedeagus slightly swollen in apical third, vesica with minute spines, one slender and two stout cornuti present, larger one usually with a more or less distinctly bifid tip.

GENITALIA ♀ (Fig. 96). Ostium bursae broad, membranous; ductus bursae long and narrow, antrum present.

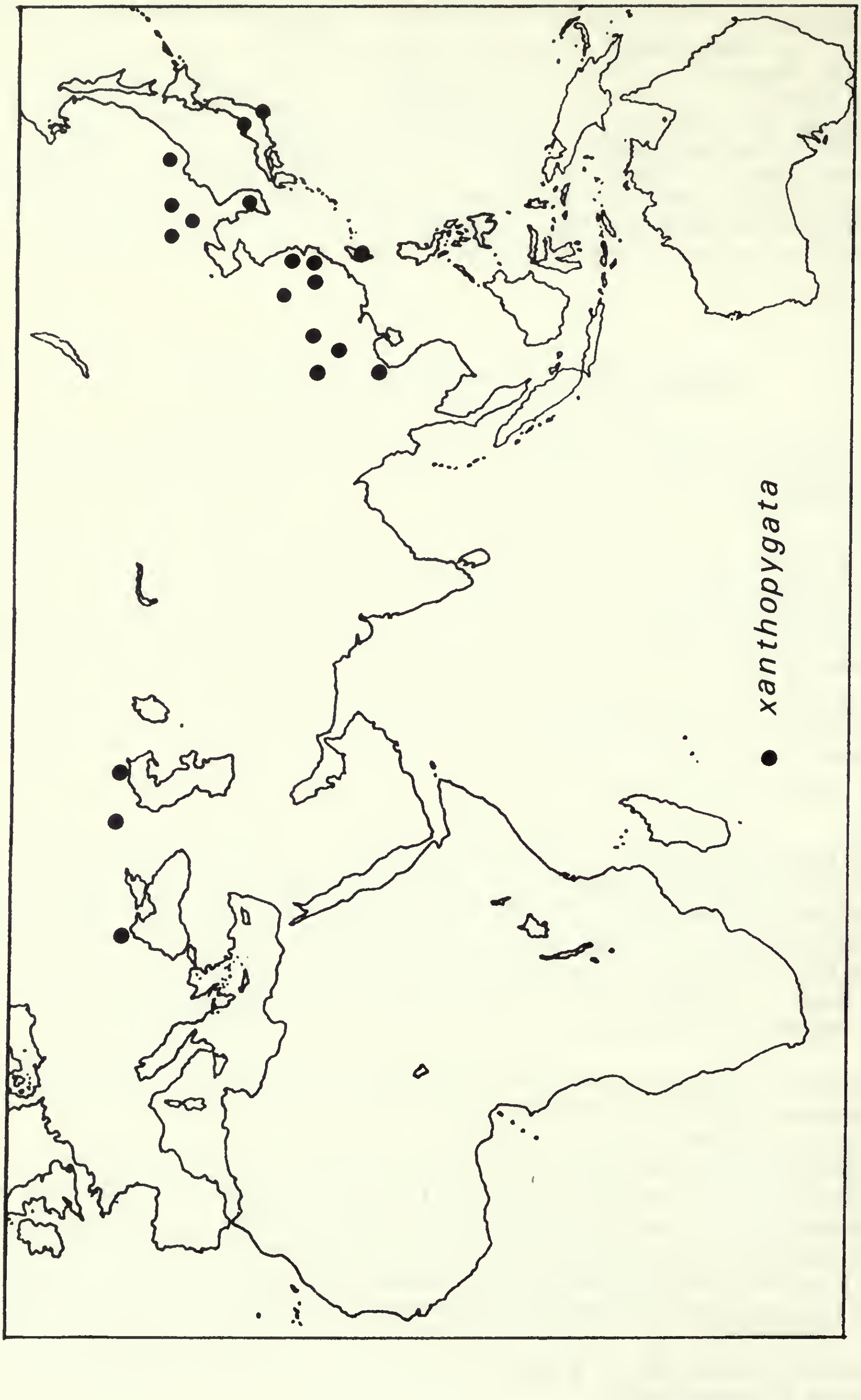
REMARKS. In general the male of *S. xanthopygata* is smaller than that of *S. praelata*, but males from the U.S.S.R are about the same size. It appears from the material examined that specimens of *S. xanthopygata* from the U.S.S.R. have in the past been misidentified as *S. praelata*, probably because of their similarity in size. By external morphology the male of *S. xanthopygata* can be distinguished from *S. praelata* by the shorter antennal cilia, which are about three-quarters of the diameter of the antennal shaft, while in *S. praelata* they are about 1·2 times its diameter. In the female of *S. xanthopygata* the anal tuft is pale ochreous yellow, while in *S. praelata* it is greyish white.

In the genitalia of the male of *S. xanthopygata* the bases of the cornuti are long, but short and stout in *S. praelata*. In the female, the ductus bursae is long and narrow in *S. xanthopygata* while in *S. praelata* it is comparatively short and broad.

The male genitalia of this species are very similar to those of *S. nivella* in which the bases of the cornuti are long, but in *S. xanthopygata* the larger one usually has a bifid tip and the vesica is lined with spines which are smaller than those in *S. nivella*. The males of *S. xanthopygata* and *S. nivella* are usually quite distinct superficially, and the latter species has markings on the forewing although in a very few specimens the markings are absent, leaving a plain ochreous forewing. In this case the two characters in the genitalia mentioned above are useful for separating these two species.

In the female genitalia, the long ductus bursae and the shape of the antrum are very characteristic of *S. xanthopygata*.

BIOLOGY. Unknown.


● xanthopygata

Map 2

DISTRIBUTION. U.S.S.R., China, Vietnam, Taiwan, Japan, Korea.

MATERIAL EXAMINED

U.S.S.R.: 1 ♀, same data as lectotype (UM, Bremen); 1 ♀, Nikolsk Ussurijsk, 21.vii.1919 (UM, Bremen); 1 ♀, Nikolsk Ussurijsk, 21,vii1919 (LN, Karlsruhe); 1 ♀, Nikolsk Ussurijsk, 30.vii[19] 19 (ZSBS, Munich) (all paralectotypes of *Scirpophaga praelata* v. *xanthopygata* Schawerda); 1 ♀, Ural, 1872 (*Haberh*[*auer*]) (NM, Vienna); 1 ♂, Sarepta (MAK, Bonn); 1 ♀, Sarepta (BMNH); 1 ♀, Ussuri Railway, Chabarovsk, 22.vii.1910 (*Barsow*) (BMNH); 1 ♂, Ukraine, 14.viii.1941 (MAK, Bonn); 1 ♂, South U.S.S.R. (BMNH); 1 ♀, no further data (NM, Vienna). **China**: 2 ♀, Harbin, 30.vii.1937 (BMNH); 1 ♀, Harbin, vii.1923 (*Tolmachov*) (MAK, Bonn); 1 ♀, Hsiolin, Manchuria, 7.vii.1937 (BMNH); 1 ♀, Djalantun, Manchuria, 23.vii.1937 (*Khingan*) (BMNH); 1 ♀, Manchuria (BMNH); 1 ♀, Sidemi (*Jankowski*) (BMNH); 1 ♂, Shanghai, ix.1892 (BMNH); 4 ♂, 6 ♀, Shanghai (MNHN, Paris); 1 ♀, Shanghai, 21.ix.1935 (MAK, Bonn); 9 ♂, 3 ♀, Hsü-Chin-Hui (Zi Kaweg) (MNHN, Paris); 1 ♂, 1 ♀, Fokien, Tinghai, vi.1899 (*Garde*) (BMNH); 2 ♂, 1 ♀, Lui Shin Tze, Hupeh Prov., viii.1912 (*Betton*) (BMNH);1 ♂, 1 ♀, Ichang, viii.1887 (*Pratt*) (BMNH); 4 ♀, Chungking, 7.viii.–11.x.1912 (*Barry*) (BMNH); 1 ♀, Shantung, Tsinan, 6.ix.1926 (*Hindle*) (BMNH); 1 ♀, Chekiang (BMNH); 1 ♀, Tien-mu-shan, Chekiang Prov., 8.vi.1932 (*Höne*) (BMNH); 1 ♀, Tapaishan, 8.viii.1936 (*Höne*) (MAK, Bonn); 1 ♂, 1 ♀, Lungtan nr Nanking, 26.vi., 27.vii.1933 (*Höne*) (LN, Karlsruhe); 5 ♂, 8 ♀, 31.v.–7.x.1933 (*Höne*) (MAK, Bonn); 2 ♂, 1 ♀, Foochow (*Yang*) (BMNH); 2 ♀, Peiping (BMNH); 1 ♂, 5 ♀, no further data (BMNH). **Vietnam**: 1 ♂, 2 ♀, Tongking, Phu-tho (MNHN, Paris); 1 ♀, Tongking, Cho-Ganh (MNHN, Paris). **Taiwan**: 1 ♀, Takow, 18.ix.1904 (*Wileman*) (BMNH). **Japan**: 2 ♀, Kashiwagi, prov. Yamato, Honshu, 26.vi.1899 (*Wileman*) (BMNH); 1 ♀, Yoshino, prov. Yamato, Honshu, 11.vii.1899 (BMNH); 1 ♂, Yokohama, 18.viii.1911 (*Höne*) (LN, Karlsruhe); 3 ♂, 5 ♀, Yokohama, 9.x.1910, 17–22.ix.1911 (*Höne*) (MAK, Bonn). **Korea**: 1 ♀, Ryong Hpieng, 1.ix.1936 (MNHN, Paris).

Scirpophaga nivella (Fabricius, 1794)
(Figs 33, 34, 97, 98, 129, 130, Map 3)

Tinea nivella Fabricius, 1794: 296; Zimsen, 1964: 577. Holotype ♀, INDIA: '*C. niveus*, ex. Ind. Or.'; 'Mus. Sch. & T. L.' (ZM, Copenhagen, genitalia slide no. 3602) [examined].

Crambus niveus (Fabricius) Fabricius, 1798: 472; Zimsen, 1964: 577.

Scirpophaga chrysorrhoa Zeller, 1863: 1; Hampson, 1895: 913; 1896: 46 (partim); Leech, 1901: 401 (partim); Martin, 1958: 189, figs 4, 8, pl. 6, figs 5, 6; Common, 1960: 314, figs 4A, 4B, 7B, pl. 1, figs 1, 2. Holotype ♀, JAVA: 'Java, Tengstr. 98'; 'Zell. Coll. 1884' (BMNH, Pyralidae genitalia slide no. 2263) [examined]. **Syn. n.**

Scirpophaga auriflua Zeller, 1863: 2; Moore, 1867: 666; 1886: 387; Hampson, 1895: 913; 1896: 46 (partim). Holotype ♀, INDIA: 'Calcutta, Staint. 3/56, Zell. Coll. 1884' (BMNH, Pyralidae genitalia slide no. 6317) [examined]. [Synonymized with *nivella* Fabricius by Caradja, 1925: 44, but erroneously cited as a senior synonym.]

Scirpophaga brunnescens Moore, 1888: 225. LECTOTYPE ♂, INDIA: Calcutta (*Atkinson*), Moore Coll. 94-106 (BMNH, Pyralidae genitalia slide no. 2466), here designated [examined]. **Syn. n.**

[*Scirpophaga butyrota* Meyrick sensu Meyrick, 1889: 520 (partim, erroneously included in type-series of *Scirpophaga butyrota*). Misidentification.]

Schoenobius celidias Meyrick, 1894: 475; Hampson, 1895: 916 (as a synonym of *Schoenobius adjurellus* Walker). LECTOTYPE ♂, BORNEO: 'S.E. Borneo, Doherty, May 91, 96-43' (BMNH, Pyralidae genitalia slide no. 2264), here designated [examined]. **Syn. n.**

Schoenobius brunnescens (Moore) Hampson, 1895: 916; 1896: 48 (as a synonym of *Schoenobius adjurellus* Walker); Caradja, 1925: 45, pl. 1, fig. 4; Shibuya, 1928: 16, 61; de Joannis, 1929: 609.

Crambus nivella (Fabricius); Aurivillius, 1898: 169.

Apurima nivella (Fabricius) Aurivillius, 1898: 173.

Scirpophaga euclastalis Strand, 1918: 262. Holotype ♂, TAIWAN ('Formosa'): Anping, v.1911 (*H. Sauter*) (IP, Eberswalde) [examined]. **Syn. n.**

Scirpophaga nivella (Fabricius) Shibuya, 1928: 61, pl. 4, fig. 27 (partim); de Joannis, 1929: 607.

♂ (Fig. 129). 21–31 mm. Ochreous. Length of labial palpus approximately 1·3 times diameter of compound eye. Forewing ochreous with four fuscous spots, three on submedian fold at about one-fifth, half and three-quarters, the fourth at lower angle of cell; an oblique irregular fuscous line extends inwards from costa near apex to third spot on fold; a series of small fuscous neural dots along termen, underside fuscous; hindwing whitish, costal area and basal half ochreous, underside ochreous in basal half.

♀ (Fig. 130). 24–40 mm. White. Fore- and hindwing white, sometimes upperside of forewing suffused with pale ochreous; frenulum double-bristled. Anal tuft ochreous yellow.

GENITALIA ♂ (Figs 33, 34). Subteguminal process large, flattened, with sinuous margin; valva rather elongate, apex more or less pointed posteriorly; aedeagus slightly swollen in apical fourth; vesica with coarse spines, one slender and two unequal long-based cornuti present.

GENITALIA ♀ (Figs 97, 98). Ostium bursae broad, membranous, wrinkled, lined with minute spines. Ductus bursae with two forms of sclerotization. In females from the Asiatic mainland south to Sumatra, the plates in the antrum are separated, and the sclerotization between the ductus seminalis and corpus bursae is usually annulated laterally and broader in diameter than the section between the ductus seminalis and ostium bursae (Fig. 97). In females from Timor to Fiji, with the exception of one specimen from Oomsis, Markham Valley, New Guinea, the plates of the antrum are fused to form a single more or less hemispherical structure, and the ductus bursae has the sclerotization smooth, non-annulated and nearly uniform in diameter (Fig. 98).

REMARKS. Moore did not mention the number of specimens in the type-series of *Schoenobius brunnescens*, but stated that they were in the collections of Staudinger and Moore. Only one syntype, here designated as lectotype, can at present be found; paralectotype material is possibly located in Staudinger's collection in Berlin.

In the male of *S. nivella*, the markings on the forewing can be variable. The three spots on the submedian fold are sometimes obsolescent but the fourth spot at the lower angle of the cell is usually prominent. In a few specimens, the markings are entirely absent, and the wing is plain ochreous. In the female the forewing is usually white, but it is sometimes suffused with pale ochreous. Cervix bursae is present in some female genitalia.

Female specimens from the Asiatic mainland, Sri Lanka, Andaman Islands, Sumatra, Borneo, Sarawak, Philippines and Taiwan, have genitalia with separate sclerotized plates in the antrum. The section of the ductus bursae between the ductus seminalis and the corpus bursae is dilated and usually wrinkled laterally (Fig. 97). On the other hand, the females from Timor, Aru Island, New Guinea (except one female from Oomsis, Markham Valley), Australia and Fiji differ in having a fused structure (Fig. 98). No difference could be found between male specimens from these two regions.

The name *S. nivella* has, until now, been erroneously used for *S. excerptalis*, and this species was known as *S. chrysorrhoa*. In superficial appearance, the male of *S. nivella* is very similar to that of *S. incertulas* in markings, but *S. nivella* can be distinguished by its shorter maxillary and labial palpi. The length of the labial palpus is about 1·3 and 3·0 times the diameter of the compound eye in *S. nivella* and *S. incertulas* respectively. The forewing of *S. incertulas* is rather dull while in *S. nivella* it is more shining.

In the male of *S. nivella*, the coarse spines on the vesica and the long-based cornuti are characteristic, while in the female the shape of the antrum is diagnostic.

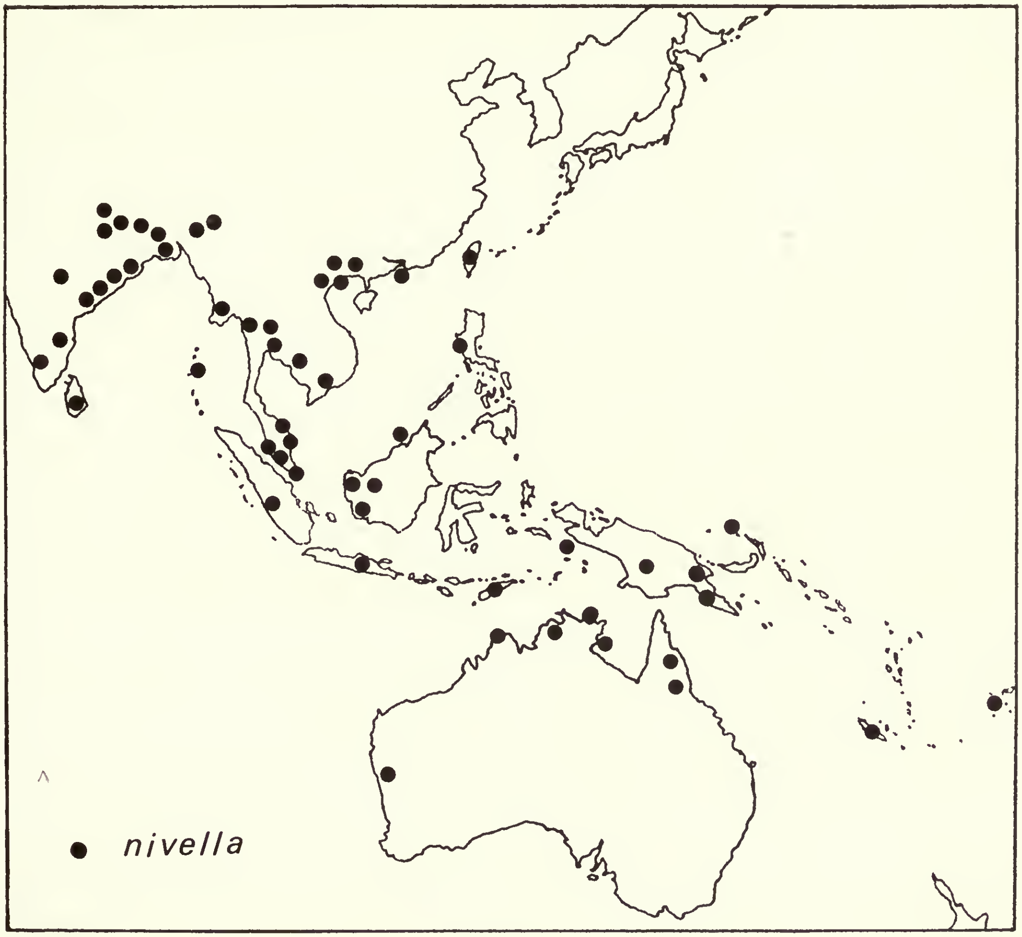
BIOLOGY (for host plants see p. 192). Many authors incorrectly referred to *Scirpophaga nivella* as a serious pest of sugar-cane. Such observations are based on misidentifications, since *S. nivella* is associated mainly with rice. The pest of sugar-cane which has the common name 'top borer' is likely to be *S. excerptalis*.

The true *S. nivella*, which was until now recorded as *S. chrysorrhoa*, is found mainly in rice fields. The males of this species have the colour and markings of the forewing very similar to those of the males of *S. incertulas*, which is a very serious pest of rice. There is no doubt that males of *S. nivella* have been misidentified as *S. incertulas* in many of the numerous publications citing the latter.

The host plants and parasites mentioned in the literature need to be checked critically. Marumo (1934) listed *Saccharum officinarum* and*Miscanthus sinensis* as the host plants of *S. nivella*. Moritsugu (1931) stated that in Taiwan, in addition to sugar-cane, the larva of *S. nivella* also feeds on *Miscanthus sinensis, Imperata cylindrica, Phragmites longivalvis, Ischaemum rugosum* and *Typha capensis*. From this list, the species that feeds on sugar-cane should be *S. excerptalis*. It is not certain whether there were any true *S. nivella*, and probably several species were involved. He also stated that the adults were not attracted to light. This is not true of *S.*

nivella and *S. excerptalis* because, in the material examined, there are specimens of both species which were caught at light. *S. nivella* recorded by Jepson (1954: 9, 20) is likely to be *S. excerptalis.*

There are many references to the life history but it is impossible to determine in most cases if they refer to the true *S. nivella*. Undoubtedly the majority of them should be ascribed to *S. excerptalis*.



Map 3

DISTRIBUTION. India, Nepal, Bangladesh, Sri Lanka, Andaman Islands, Burma, Thailand, Vietnam, China, Hong Kong, Taiwan, West Malaysia, Singapore, Philippines, Sumatra, Java, Borneo, Timor, Aru Island, New Guinea, Australia, New Caledonia, Fiji.

MATERIAL EXAMINED

India: 7 ♂, Calcutta, 1858 (*Atkinson*) (BMNH); 4 ♂, Calcutta (MNHN, Paris); 3 ♂, 1 ♀, Calcutta, 5.vii.–27.x.1934, x.1890 (BMNH); 2 ♀, Calcutta (BMNH); 1 ♂, 1 ♀, Barrackpur (BMNH); 1 ♂, Barrackpur (MNHN, Paris); 1 ♂, 1 ♀, Barrackpur, 9.i.1886 (UM, Oxford); 1 ♀, Bihar, 11.viii.1915 (*Boyd*) (BMNH); 1 ♀, Bihar, at light, 17.x.1933 (*Batra*) (BMNH); 4 ♀, Godavari Dist., Samalkot, at light, xii.1925 (BMNH); 2 ♀, Bhubaneswar, at rest on *Cyperus* sp. (BMNH); 2 ♀, Bhubaneswar, at rest on *Oryza sativa*, 18, 28.iv.1962 (NMNH, Washington); 1 ♀, Bhubaneswar, on *Scirpus* sp., xi.1963 (BMNH); 1 ♂, Orissa (BMNH); 1 ♂, 1 ♀, Munghal Sarai, 6–12.iv.1904 (*Betton*) (BMNH); 1 ♂, 2 ♀, Lucknow, 400 ft [120 m], at light, 8.xi.1937, 1–14.viii.1938 (*Graham*) (BMNH); 1 ♀, Cochin, 27.xii.1941 (*Graham*) (BMNH); 1 ♀, Ganjam (*Elwes*) (BMNH); 2 ♀, Assam, at rest on *Scirpus* sp., iii.1963 (BMNH); 1 ♂, Assam (BMNH); 1 ♀, Madras, vii.1897

(BMNH); 1 ♀, Jorhat, in rice-field, viii.1962 (BMNH); 1 ♂, no further data (UM, Oxford); 6 ♀, no further data (BMNH). **Nepal**: 15 ♂, 9 ♀, Rapti Tal, Megouli, 300 m, 29.iii.–4.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich); 1 ♀, Rapti Tal, Jhawani, 200 m, 15.v.1967 (*Dierl-Forster-Schacht*) (ZSBS, Munich); 1 ♀, Katmandu, 1400 m, 9.vi.1962 (*Ebert & Falkner*) (ZSBS, Munich); 1 ♂, Bhimpedi, 400 m, 4–7.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich). **Bangladesh**: 1 ♂, Dacca, on *Oryza sativa*, 1964 (BMNH); 1 ♂, Bengal, 27.vii.1911 (*Fletcher*) (BMNH). **Sri Lanka**: 1 ♂, Galgamma, x.1907 (BMNH); 3 ♂, 7 ♀, Colombo, 14.iv.1898, x.1901, vii.1907, viii.1908, ix.1911 (BMNH); 1 ♀, Bodurelia (*Penther*) (NM, Vienna); 4 ♂, Hambantota (BMNH); 1 ♀, Mirigama (BMNH); 4 ♂, Puttalam (BMNH); 1 ♂, Tricomali, 10.i.1908 (*Meade Waldo*) (BMNH); 1 ♀, iii.1891 (BMNH); 1 ♂, 2 ♀, no further data (BMNH). **Andaman Islands**: 2 ♀, Port Blair, xii.1904–i.1905 (BMNH); 1 ♂, Port Blair, 18.iii.1925 (*Mujtaba*) (BMNH); 3 ♂, 20 ♀, no precise locality, i.1904 (BMNH). **Burma**: 1 ♀, Mergui (BMNH); 1 ♀, Kadan Kyun (King Island) (*Bott*) (BMNH); 2 ♂, Rangoon, vii.–viii.1889 (BMNH); 1 ♂, 4 ♀, Rangoon (BMNH); 1 ♂, 1 ♀, Lower Burma (BMNH). **Thailand**: 2 ♂, 2 ♀, Bangkok, in rice-fields, 25.xii.1967, 23.i.–6.iii.1968 (*Hattori*) (DA, Bangkok); 1 ♀, Bangkok (*Aagaard*) (BMNH); 1 ♀, Bangkok, at light, 22.vi.1951 (*Vorasap*) (DA, Bangkok); 3 ♀, 18.viii.–3.ix.1924 (BMNH); 4 ♀, 1–31.v.1926 (*Ladell*) (BMNH); 1 ♀, Bangkok, 1.iii.1954 (*Munyeekul*) (DA, Bangkok); 1 ♂, 1 ♀, Bangkok, 1.xi.1948 (*Pholboon*) (DA, Bangkok); 2 ♀, Bangkok, 5.viii.1963, 24.ix.1970 (DA, Bangkok); 1 ♀, Bangkok, 20.ix.1965 (*Bänzinger*) (BMNH); 1 ♀, Bangkok (*Smith*) (NMNH, Washington); 5 ♀, Rangsit, 2.vi.–6.xi.1926 (DA, Bangkok); 1 ♂, Rangsit, xi.1966 (DA, Bangkok); 1 ♂, Prathumthani, at light, 10.ii.1963 (*Paranatee*) (NMNH, Washington); 3 ♀, Cholburi, 20.ix.1954 (*Grohs*) (DA, Bangkok); 2 ♀, Chantaburi, 6–17.xii.1955 (*Pholboon*) (DA, Bangkok); 1 ♂, 3 ♀, Chantaburi, 1–7.ii.1958 (*Arunin*) (DA, Bangkok); 1 ♂, Kanchanaburi, 26.ix.1955 (*Lekakul*) (DA, Bangkok); 3 ♀ Minburi, ix.1935 (*Penchitr*) (DA, Bangkok); 2 ♂, 2 ♀, no further data (BMNH); 4 ♂, 8 ♀, 10.ii.–10.v.1962 (*Friedel*) (ZSBS, Munich). **Vietnam**: 4 ♂, 6 ♀, Tongking, Choganh (MNHN, Paris); 3 ♀, Hanoi (MNHN, Paris); 1 ♀, Hanoi, iv.–vi.1904 (MNHN, Paris); 1 ♀, Haiphong (BMNH); 4 ♀, Saigon (MNHN, Paris); 3 ♀, Cochin China (MNHN, Paris). **China**: 1 ♂, Kwangtung, 6.xi.1934 (*Chiu*) (BMNH). **Hong Kong**: 2 ♂, Lamti, on *Eleocharis* sp., 15.ix.1961 (*So*) (BMNH). **Taiwan**: 11 ♀, Suishako, 1907 (BMNH); 1 ♀, Tainan, 1.iv.1905 (*Wileman*) (BMNH); 8 ♀, Takow, 4.ix.–30.x.1904 (*Wileman*) (BMNH); 2 ♀, Tingan, Hainan, vi.1905 (BMNH). **West Malaysia**: 4 ♀, Penang, xi.1896 (*Curtis*) (BMNH); 4 ♂, Port Dickson, at light, 19.iii.1927, 12.–18.i.1941 (BMNH); 1 ♀, Kelantan, 28.vii.1926 (BMNH); 1 ♀, Bukit Tangga, 28.i.1919 (*Laverock*) (BMNH); 1 ♀, Pahang, at light, 19.vii.1925 (*Evans*) (BMNH); 1 ♀, Selangor, 22.vii.1825 (*Seimund*) (BMNH); 2 ♀, Kuala Lampur, 19.i., 4.iii.1924 (BMNH); 1 ♀, Kuala Lumpur, xii.19--(*Kloss*) (BMNH); 2 ♀, Butterworth, 19.xii.1969 (BMNH); 1 ♀, Malacca, 18.ii.1903 (*Meade Waldo*) (BMNH). **Singapore**: 1 ♂, 7 ♀, no further data (*Ridley*) (BMNH); 1 ♀, ii.–iv.1906 (*Ridley*) (UM, Oxford). **Philippines**: 3 ♂, 32 ♀, 7.i., 9.iii., 8.xi., 24.xii.1913 (*Wileman*) (BMNH); 1 ♀, Manila (MNHN, Paris); 1 ♂, 1 ♀, Tarlic (*Browne*) (BMNH). **Sumatra**: 1 ♀, Padang (BMNH). **Borneo**: 1 ♂, 'S.E. Borneo, WD. 5/91' (BMNH) (paralectotype of *Schoenobius celidias* Meyrick); 17 ♀, Sarawak, Paya Paloh, at light, 3.iv.–17.v., 13.xii.1967 (*Rothschild*) (BMNH); 7 ♀, Sarawak, on *Oryza sativa*, 18.iii.1966 (*Rothschild*) (BMNH); 1 ♀, Sarawak, Simanggang, 13.x.1962 (*Wallace*) (BMNH); 2 ♀, Sarawak, Pruan, 12.x.1962 (*Wallace*) (BMNH); 4 ♂, 8 ♀, Sarawak (BMNH); 1 ♂, Kuching (UM, Oxford); 1 ♀, Kretam, 21.xi.1950–i.1951 (*Hedley*) (BMNH); 1 ♀, Labaun, xi.1911 (*Everett*) (BMNH). **Timor**: 9 ♂, Suai, 7–31.xii.1912, 15–21.i.1913 (*Wahr*) (BMNH). **Aru Island**: 1 ♀, iv.–vii.1896 (*Webster*) (BMNH). **New Guinea**: 1 ♂, Port Moresby, 28.i.1913 (*Garson*) (UM, Oxford); 1 ♀, Port Moresby, 1888 (BMNH) (paralectotype of *Scirpophaga butyrota* Meyrick); 1 ♀, Port Moresby (BMNH); 2 ♀, St Joseph River (*Weiske*) (BMNH); 1 ♂, St Matthias I., vii.1923 (*Eichhorn*) (BMNH); 1 ♀, Oomsis, Markham Valley, 100 ft [30 m], 31.viii.1957 (*Munroe & Holland*) (BMNH); 7 ♂, 1 ♀, Digoel R. (*Vertenten*) (ZM, Amsterdam). **Australia**: 1 ♂, 2 ♀, Port Darwin, 6.vi.–2.vii.1922 (*Wilson*) (BMNH); 3 ♀, Port Darwin, vi.1890, vii.1891 (BMNH); 1 ♂, Port Darwin, 1910 (*Dodd*) (BMNH); 1 ♂, 1 ♀, Port Darwin (BMNH); 1 ♂, Cassini I., v.1891 (BMNH); 1 ♀, Groote Eylandt I., 26.i.1925 (*Wilkins*) (BMNH); 1 ♀, Crocodile I., 26.xii.1925 (*Wilkins*) (BMNH); 1 ♂, 1 ♀, Mackay, Queensland (BMNH); 1 ♂, Cooktown, Queensland (BMNH); 1 ♂, Geraldton, Queensland (BMNH); 1 ♀, Queensland (BMNH). **New Caledonia**: 1 ♀, 1939 (MNHN, Paris). **Fiji**: 1 ♂, Vunidawa, 14.ii.1933 (BMNH); 1 ♀, Koronivia, at light, 26.x.1962 (BMNH); 5 ♀, ix.1966,1967 (*Robinson*) (BMNH); 1 ♀, no further data (NMNH, Washington).

Scirpophaga parvalis (Wileman, 1911)

(Figs 37, 38, 99, 131, 132, Map 4)

Schoenobius costalis var. *parvalis* Wileman, 1911: 355. Holotype ♂, JAPAN: Yokohama, prov. Musashi, Honshu Plains, 12.viii.1898 (*A. E. Wileman*) (BMNH, Pyralidae genitalia slide no. 6343) [examined].

[*Scirpophaga auriflua* Zeller sensu Leech, 1901: 401 (partim). Misidentification.]

Scirpophaga parvalis (Wileman) Shibuya, 1931: 368; Marumo, 1934: 2, 15, pl. 1, figs 4, 5.

♂ (Fig. 131). 20–25 mm. Pale ochreous white. Length of labial palpus approximately 1·2 times diameter of compound eye. Forewing pale ochreous white, underside fuscous; hindwing pale ochreous white, underside suffused with fuscous in costal half.

♀ (Fig. 132). 25–31 mm. White. Fore- and hindwing white on both surfaces; frenulum double-bristled. Anal tuft white.

Genitalia ♂ (Figs 37, 38). Subteguminal process large, flattened, rounded, with smooth margin; valva nearly truncate; aedeagus swollen in apical third, vesica with minute spines, one slender and three stout cornuti present.

Genitalia ♀ (Fig. 99). Ostium bursae broad, membranous, wrinkled; ductus bursae broad, section between ostium bursae and ductus seminalis expanded, slightly evaginated medially, and that between ductus seminalis and corpus bursae more or less uniform in diameter.

Remarks. The male of *S. parvalis* is similar externally to that of *S. xanthopygata* in general coloration and size, and the two may be confused since they are overlapping in their distribution (Manchurian Subregion). In general, the frons of *S. parvalis* is more convex than that of *S. xanthopygata,* but as there is a certain amount of variation, it can be almost identical. The ventral cilia of the antenna in *S. parvalis* are about the same in length as the diameter of the antennal shaft, while in *S. xanthopygata* they are only about three-quarters of the diameter. This seems at present to be the most useful character separating these two species externally.

S. parvalis can be distinguished from the other white species by the genitalic structures. In the male, the subteguminal process is rounded and there are four cornuti in the aedeagus. In the female, the ductus bursae is broad and heavily sclerotized, and thus cannot be confused with that of the other species.

Biology. Unknown.

Distribution. Japan, North Korea, South Korea, China.

Material examined

Japan: 2 ♀, same data as holotype (BMNH), 4 ♂, same data as holotype, 3.viii.1898 (BMNH), 1 ♀, same data as holotype, 10.viii.1898 (BMNH), 1 ♀, Tokyo, Musashi, Honshu Plain, 10.ix.1893 (all paratypes of *Schoenobius costalis* var. *parvalis* Wileman) (BMNH); 1 ♀, Kobe, vi.1913 (*Höne*) (MAK, Bonn); 1 ♂, Kyushu, 8.vi.1958 (*Yoshii*) (CNC, Ottawa); 1 ♀, Nikko, prov. Shimotsuke, Honshu, 2000 ft. [600 m], 5.viii.1893 (*Wileman*) (BMNH); 1 ♀, Sakata, viii.1896 (*Leech*) (BMNH); 25 ♂, 24 ♀, Yokohama, 27.viii.1910–28.vii.1912 (*Höne*) (MAK, Bonn); 14 ♂, 5♀, Yokohama, 27.vi.1910–viii.1912 (*Höne*) (LN, Karlsruhe); 1 ♀, no further data (BMNH). **Korea (North)**: 1 ♀, Wonsan (Gensan), 9.vii.1897 (*Fletcher*) (BMNH); 2 ♀, Oridong, 1–7.x.1953 (*Thompson*) (BMNH). **Korea (South)**: 1 ♂, 3 ♀, Inchon (Chemulpho), 5–21.viii., 10.ix.1944 (*Howarth*) (BMNH). **China**: 2 ♀, Harbin, 6–29.vii.1952 (*Alin*) (BMNH); 1 ♀, Hsiaoling, 16.viii.1939 (ZSBS, Munich); 12 ♂, 3 ♀, Foochow, 1936–38 (*Yang*) (BMNH); 1 ♀, Peiping (BMNH); 1 ♀, Shanghai (BMNH); 1 ♀, Shanghai (MNHN, Paris); 1 ♀, Hsü-Chia-Hui (Zi Kaweg) (MNHN, Paris).

Scirpophaga phaedima Common, 1960

(Figs 35, 36, 133, Map 4)

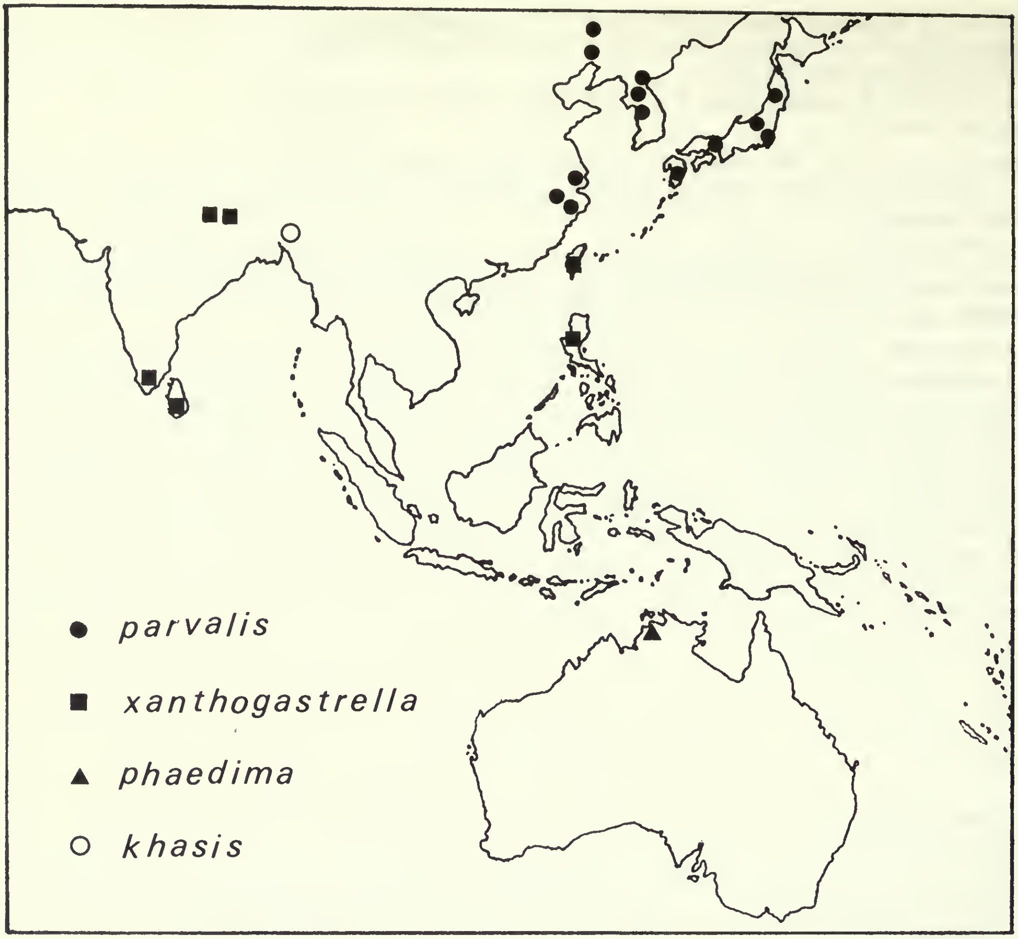
Scirpophaga phaedima Common, 1960: 317, Figs 4C, 4D, pl. 2, Fig. 1. Holotype ♂, Australia: P. Darwin, Jan. [19]09 (*F. P. Dodd*) (ANIC, Canberra, genitalia slide no. P15) [examined].

♂ (Fig. 133). 22·4 mm. White. Length of labial palpus approximately 1·6 times diameter of compound eye. Fore- and hindwing white, underside pale fuscous.

♀. Unknown.

Genitalia ♂ (Figs 35, 36). Uncus and gnathos relatively short; subteguminal process large, flattened, with sinuous margin; valva pointed posteriorly; aedeagus slender, expanded towards apex, vesica with coarse spines, one slender and two stout cornuti present.

Remarks. Only the male holotype has been examined during the present study. Common (1960) mentions two other male specimens from Silver Plains, Cape York Peninsula, Australia.



Map 4

The male genitalia of this species are very similar to those of *S. nivella* but the uncus and gnathos are relatively shorter and the dorsal sclerotized thickening of the tegumen is square. The uniformly white forewing and smaller size of *S. phaedima* readily distinguish this species from *S. nivella,* which has the forewing ochreous and with markings.

Biology. Unknown.

Distribution. Australia.

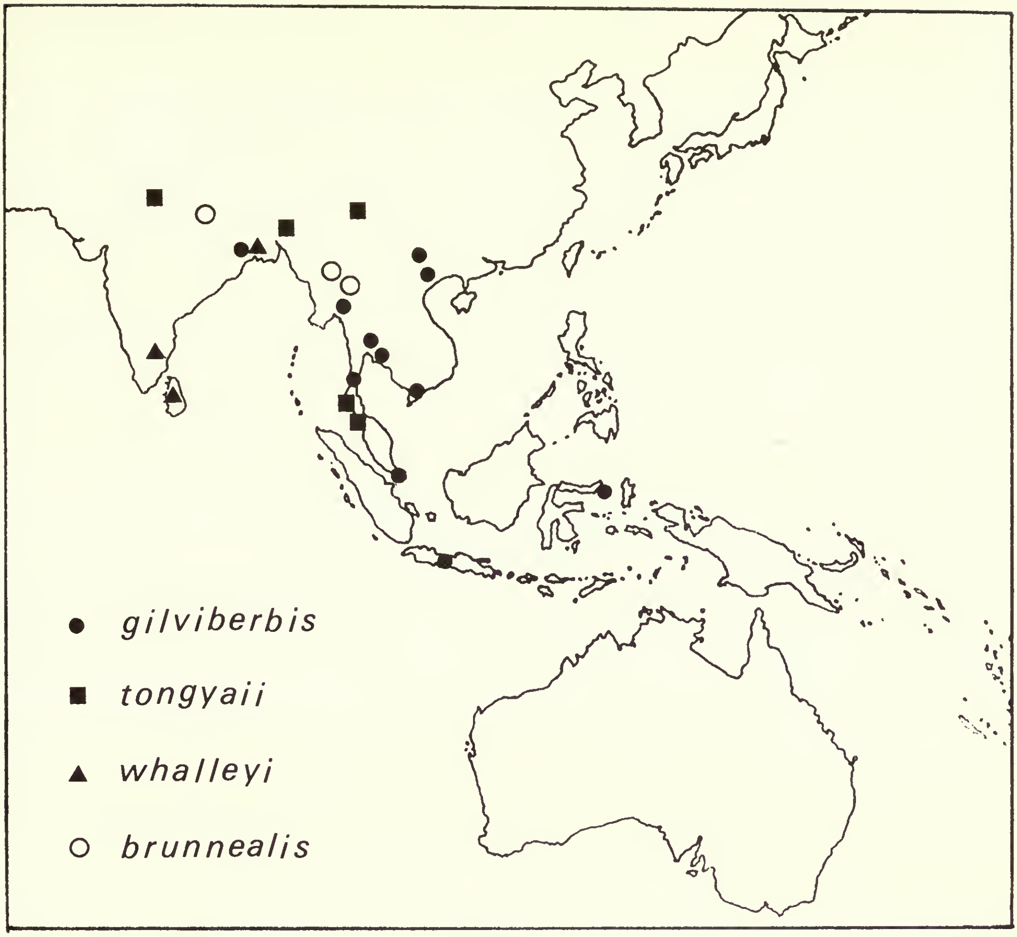
Scirpophaga gilviberbis Zeller, 1863 **comb. rev.**

(Figs 41, 42, 101, 134, 135, Map 5)

Scirpophaga gilviberbis Zeller, 1863:2; Walker, 1864:968; Moore, 1867: 666; Hampson, 1895:913; 1896: 46 (partim); de Joannis, 1929: 607. Holotype ♀, India: [Calcutta] (BMNH, Pyralidae genitalia slide no. 5024) [examined].

Niphadoses gilviberbis (Zeller) Common, 1960: 327; Kapur, 1967: 6, 22.

♂ (Fig. 134). 20–22 mm. Dark ochreous. Length of labial palpus approximately 1.5 times diameter of compound eye. Forewing ochreous with sparse fuscous scales, markings as in *S. nivella;* underside fuscous; hindwing white, costal area and apex ochreous.



Map 5

♀ (Fig. 135). 23–35 mm. White. Fore- and hindwing white, sometimes suffused with ochreous; frenulum single-bristled. Anal tuft whitish grey to dark grey.

Genitalia ♂ (Figs 41, 42). Uncus and gnathos relatively long and slender, gnathos arms converging gradually; subteguminal process flattened, rounded, with smooth margin; valva with costal and ventral margins nearly straight and parallel, distal margin rounded; aedeagus slender, one tridentate and two stout cornuti present.

Genitalia ♀ (Fig. 101). Ostium bursae broad, membranous; ductus bursae without antrum, section between ostium bursae and ductus seminalis with sclerotized plates U-shaped in cross section; corpus bursae with small spines, denser in basal two-thirds.

Remarks. This species differs from those of the *praelata*-section in that the female has only a single-bristled frenulum and the ductus bursae is without an antrum. Before this work was undertaken, only the female was known. Common (1960) placed *gilviberbis* in the genus *Niphadoses* which he erected to include four other species, viz. *palleucus, hoplites, elachia* and *chionotus*.

The present study has shown that *gilviberbis* does not belong in *Niphadoses*. In *S. gilviberbis* vein R_1 of the forewing is not anastomosed with *Sc*, and the scales on the labial palpus are smooth and not spreading as in *Niphadoses*. In the female genitalia, the shape of the sclerotized lining of the ductus bursae is similar to that of *Niphadoses* but the ductus seminalis arises from the ductus bursae at the middle and not close to the ostium bursae. Most important is the presence of the group of setae ventro-laterally on the 8th tergite; this is characteristic of the *praelata*-group. The structure of the male genitalia supports the inclusion of *gilviberbis* in the *praelata*-group.

Much work has been published under the name *gilviberbis*. Whether the specimens referred to are true *gilviberbis* or not remains, in most cases, to be checked. The male is similar externally to *S. nivella* and *S. incertulas*, especially in the markings of the forewings, but the genitalia are quite distinct. In the female of *gilviberbis*, the genitalia are rather similar to those of Australian species which also have only a single-bristled frenulum and the ductus bursae without an antrum. The tapering towards both the ostium bursae and the ductus seminalis of the sclerotized plates in the ductus bursae is characteristic of *gilviberbis*.

BIOLOGY. According to the label data of the material examined this species is found mainly in rice fields in Thailand. Fletcher (1917: 174; 1921: 76) and Shroff (1920: 342) reported finding this species commonly in paddy fields in lower Burma.

DISTRIBUTION. India, Burma, Thailand, Vietnam, Singapore, Java, Sulawesi.

MATERIAL EXAMINED

India: 1 ♀, Calcutta, 1858 (*Atkinson*) (BMNH); 1 ♀, Barrackpur (BMNH). **Burma**: 1 ♀, Rangoon (BMNH). **Thailand**: 1 ♀, Bangkok, 3.ix.1924 (BMNH); 1 ♀, Bangkok, in rice-fields, 10.ii.1963 (NMNH, Washington); 1 ♀, Bangkok, in rice-field, 23.ii.1969 (*Hattori*) (DA, Bangkok); 1 ♀, Bangkok, at light, 1–31.xii.1968 (*Pholboon*) (DA, Bangkok); 1 ♀, Bangkok, 20.xi.1956 (*Boonprasert*) (DA, Bangkok); 2 ♂, 1 ♀, Bangkok, 8–29.xii.1967 (*Hattori*) (DA, Bangkok); 2 ♂, Rangsit, at light, 27.i.1927 (DA, Bangkok); 2 ♀, Rangsit, 2.vi.1926 (*Ladell*) (BMNH); 1 ♂, 1 ♀, Rangsit, in rice-field, 10.i.1968 (*Hattori*) (DA, Bangkok); 1 ♀, Rangsit, 30.ix.1967 (*Hattori*) (DA, Bangkok); 2 ♀, Cholburi, 20.ix.1954 (*Grohs*) (DA, Bangkok); 1 ♀, Krabi, 1–14.iii.1962 (*Friedel*) (ZSBS, Munich); 1 ♀, no further data (*Ladell*) (BMNH). **Vietnam**: 2 ♀, Hanoi (MNHN, Paris); 1 ♀, Tongking, Choganh (MNHN, Paris); 2 ♂, Cochin China (MNHN, Paris). **Singapore**: 2 ♀, no further data (*Ridley*) (BMNH). **Java**: 1 ♀, no further data (RNH, Leiden). **Sulawesi**: 2 ♀, Soengei Liat., Bangka I. (BMNH).

Scirpophaga percna Common, 1960

(Figs 43, 44, 102, 136, 137, Map 6)

Scirpophaga percna Common, 1960: 325, figs 5E, 5F, 7G, pl. 1, fig. 11. Holotype ♂, AUSTRALIA: DARWIN N.T. (*G. F. Hill*) (ANIC, Canberra, genitalia slide no. P122) [not examined].

♂ (Fig. 136). 22–25 mm. Ochreous. Length of labial palpus approximately 1·6 times diameter of compound eye. Forewing ochreous with dark fuscous markings, underside fuscous; hindwing white with fuscous suffusion in costal half, stronger on underside.

♀ (Fig. 137). 24–37 mm. White. Forewing suffused with pale ochreous, underside white; hindwing white; frenulum single-bristled. Anal tuft ochreous white.

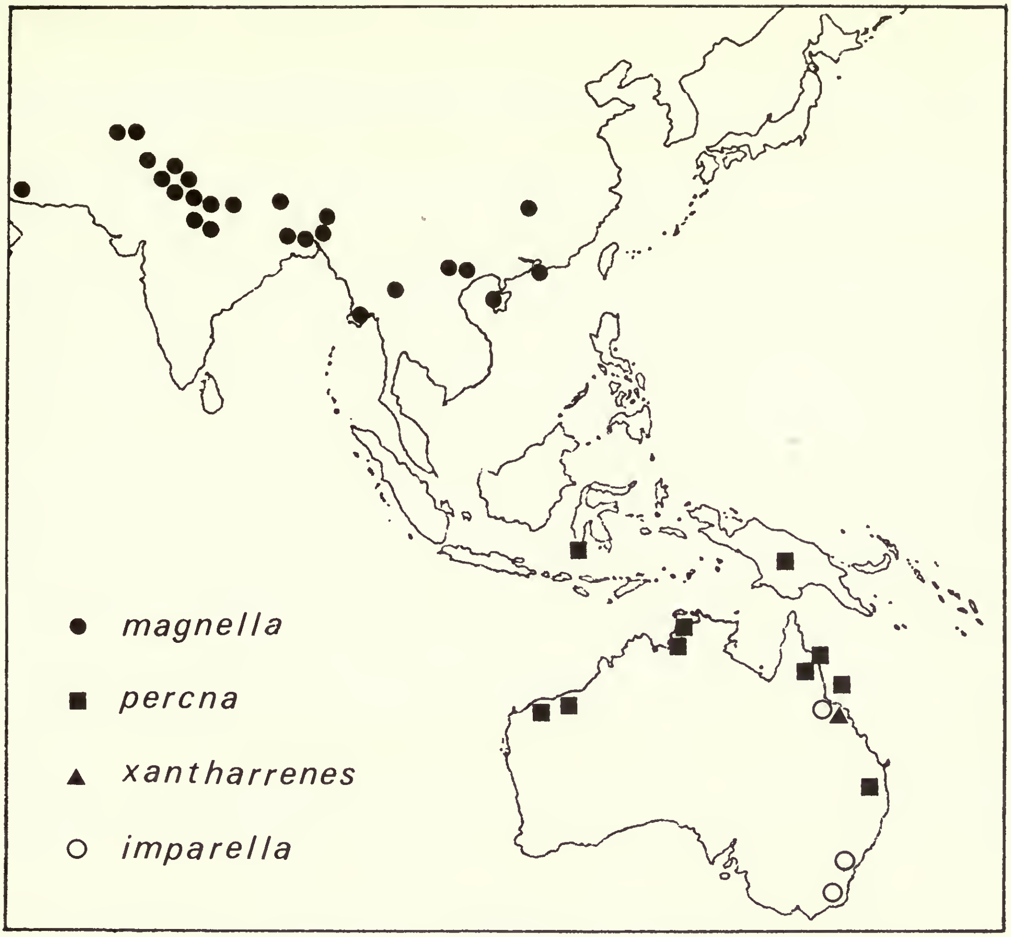
GENITALIA ♂ (Figs 43, 44). Uncus and gnathos long, slender, gnathos arms converging gradually; subteguminal process lobe-like with finely serrated margin; valva broad; aedeagus slender, vesica with minute spines, one slender and three stout cornuti present.

GENITALIA ♀ (Fig. 102). Ostium bursae broad; ductus bursae without antrum, section between ostium bursae and ductus seminalis lined with sclerotized plates towards ductus seminalis, U-shaped in cross section.

REMARKS. The markings on the forewing of the male of *S. percna* are similar to those of *S. imparella*, but the ground colour in *S. percna* is more ochreous. In the male genitalia, the uncus and gnathos are long and the valva is relatively broad. In the female the section of the ductus bursae between the ostium bursae and ductus seminalis is lined with U-shaped sclerotized plates, as in *S. xantharrenes* and *S. imparella*, but the underside of the forewing of *S. percna* is not suffused with fuscous as in the two former species.

BIOLOGY. At rest on stems of *Eleocharis dulcis* (Common, 1960).

DISTRIBUTION. Sulawesi, New Guinea, Australia.



Map 6

Material examined

Sulawesi: 1 ♂, Maros (RNH, Leiden). **New Guinea**: 12 ♂, 8 ♀, Digoel River, 1924 (*Vertenten*) (ZM, Amsterdam). **Australia**: 1 ♂, 1 ♀ (paratypes), Humpty Doo, N.T., 2.iv.1959 (*I. F. B. Common*) (BMNH, Pyralidae genitalia slide nos 6315, 6316); 1 ♂, Queensland, 27.iii.1900 (BMNH); 1 ♂, Q., Cooktown (BMNH); 1 ♂, Q., Cedar Bay (*Meek*) (BMNH); 1 ♂, 1 ♀, Q., Salisbury Plains, Boden (*Simson*) (BMNH); 1 ♂, Q., Sherlock River (*Clements*) (BMNH); 1 ♂, Q., Roebourne (BMNH); 1 ♀, Q., Percy I. (BMNH).

Scirpophaga imparella (Meyrick, 1878)
(Figs 45, 46, 103, 138, 139, Map 6)

Schoenobius imparellus Meyrick, 1878: 176; 1885: 437; 1887: 208. Lectotype ♂, Australia: 'Sydney, N. S. Wales, 8/3/78' (BMNH, Pyralidae genitalia slide no. 6311), designated by Common (1960: 321) [examined].

Scirpophaga imparella (Meyrick) Hampson, 1895: 914; Common, 1960: 321, figs 5A, 5B, 7E, pl. 1, figs 7, 8.

Scirpophaga helodes Common, 1960: 323, figs 5C, 5D, 7F, pl. 1, figs 9, 10. Holotype ♂, Australia: 'Dingo Q., 19 Mar. 1958'; 'at rest on *Eleocharis dulcis*' (*I. F. B. Common*) (ANIC, Canberra, genitalia slide no. P121) [examined]. **Syn. n.**

♂ (Fig. 138). 23–29 mm. Ochreous brown. Length of labial palpus approximately 2·6 times diameter of compound eye. Forewing ochreous brown to dark fuscous, with markings, underside fuscous; hindwing white, underside fuscous.

♀ (Fig. 139). 30–38 mm. White. Forewing white, sometimes with pale ochreous suffusion, underside fuscous; hindwing white; frenulum single-bristled. Anal tuft ochreous white.

GENITALIA ♂ (Figs 45, 46). Gnathos arms converging abruptly; subteguminal process rounded, with very fine serrated margin and scale-like projection on outer surface; aedeagus slender, one slender and three stout cornuti present.

GENITALIA ♀ (Fig. 103). Ostium bursae broad, membranous; ductus bursae without antrum, section between ostium bursae and ductus seminalis lined with sclerotized plate, U-shaped in cross section.

REMARKS. As mentioned by Meyrick (1878), this species is 'extremely variable' in both sexes. In the male, the colour of the forewing varies from ochreous brown to dark fuscous; the markings are also variable and sometimes obsolescent, leaving an almost plain-coloured forewing. Meyrick described the colour of the forewing in the female as 'satiny-white, sometimes more or less strongly suffused throughout with whitish-ochreous'. In the material examined the colour of the forewing in the female varies from pure white to ochreous, and the colour of the anal tuft corresponds with the colour of the forewing.

Common (1960) described a new species, *Scirpophaga helodes*, which is here considered to be conspecific with *S. imparella*. He mentioned that the size of *S. helodes* was usually smaller than that of *S. imparella*. His measurements of the wing expanse of *S. helodes* are: '♂ 20·9–24·2 mm., ♀ 25·8–32·4 mm.' and of *S. imparella*: '♂ 24·2–33·6 mm., ♀ 34·8–48·0 mm.' Common stated that in the male of *S. helodes*, the colour and markings were very variable, as in *S. imparella*, but the females were white and 'appear to be extremely uniform in size and coloration'. From Common's measurements it is obvious that in the female, the largest size of *S. helodes* does not exceed the smallest size of *S. imparella*. In the material examined there are females which have the wing expanse in the same range as *S. helodes*, but instead of being white the forewing is suffused with ochreous as in *S. imparella*. There is no doubt that in the female of this species the size and coloration are very variable.

With regard to the genitalia, Common separated *S. helodes* from *S. imparella* by the following characters: 'the arms of the gnathos [in *S. helodes*] are less abruptly united and the subteguminal processes lack the scale-like surface projection and distinct marginal serrations found in *S. imparella*'. This is true for the holotype and one paratype of *S. helodes* in both of which the subteguminal process appears to have a smooth margin, but under the phase-contrast microscope it is seen to have a serrated margin. In the other paratype, a scale-like surface and serrate margin of the subteguminal process are more obvious than those in the holotype of *S. imparella*. The presence or absence of a scale-like surface and a distinctly serrate margin to the subteguminal process thus appears to be due to individual variation within a single species. No difference could be found in the female genitalia. *S. helodes* was found resting on the stem of *Eleocharis sphacelata*, as also was *S. imparella*. For these reasons *S. helodes* is here considered to be synonymous with *S. imparella*.

BIOLOGY. At rest on *Eleocharis dulcis* (from the label-data of the holotype of *S. helodes*) (Australia). *Juncus prismatocarpus* (Meyrick, 1878; but Common (1960) doubted this host plant); *Heleocharis sphacelata* (Meyrick, 1887); at rest on *Cladium articulatum*, *Eleocharis sphacelata* (Common, 1960); *Eleocharis dulcis* (Common, 1960, cited under the name *Scirpophaga helodes*).

DISTRIBUTION. Australia.

MATERIAL EXAMINED

Australia: 1 ♂, 3 ♀, New South Wales, Sydney, 8.iii.1878 (BMNH) (paralectotypes of *Schoenobius imparellus* Meyrick); 1 ♂, 2 ♀, Queensland, 12 mls [19 km] E. of Duaringa, 18.iii.1958 (*Common*) (ANIC, Canberra), 1 ♂, Q., Dingo, 19.iii.1958, at rest on *Eleocharis dulcis* (*Common*), 1 ♀, Q., 12 mls [19 km] E. of Duaringa, 4.iv.1957 (*Common*) (allotype and paratypes of *Scirpophaga helodes* Common) (ANIC, Canberra; BMNH); 5 ♀, New South Wales, Nowra, xi.1924 (*Rodway*) (BMNH); 5 ♀, Queensland (BMNH); 4 ♂, 7 ♀, SE. Australia (BMNH); 1 ♀, SE. Australia (MNHN, Paris); 3 ♂, 3 ♀, no locality. 8.iii.1878 (BMNH); 2 ♀, no further data (BMNH).

Scirpophaga xantharrenes Common, 1960
(Figs 47, 48, 104, 140, 141, Map 6)

Scirpophaga xantharrenes Common, 1960: 320, figs 4G, 4H, 7D, pl. 1, figs 3, 4. Holotype ♂, AUSTRALIA: '12 mls [19 km] E. of Duaringa, Q., 18 Mar. 1958' (*I. F. B. Common*) (ANIC, Canberra, genitalia slide no. P124 [not examined].

♂ (Fig. 140). 27–28 mm. Light orange-yellow. Length of labial palpus approximately 1·4 times diameter of compound eye. Forewing light orange-yellow, costa fuscous, underside fuscous; hindwing white, terminal half and underside fuscous.

♀ (Fig. 141). 34 mm. White. Forewing white, costal margin tinged with fuscous, underside fuscous in basal three-quarters, area between costal and subcostal vein white; hindwing white, underside fuscous; frenulum single-bristled. Anal tuft orange-yellow.

GENITALIA ♂ (Figs 47, 48). Uncus and gnathos slender, gnathos arms converging abruptly, subteguminal process large, flattened, with smooth margin; valva short, truncate; aedeagus slender, one slender and two stout cornuti present.

GENITALIA ♀ (Fig. 104). Ostium bursae relatively broad, wrinkled; ductus bursae without antrum, section between ostium bursae and ductus seminalis lined with sclerotized plate, tapering towards ductus seminalis, U-shaped in cross-section.

REMARKS. This species is known only from Australia. The male can be separated from the other Australian species of the group by the light orange-yellow colour of the forewing and the fuscous line along the costa. In the genitalia, the gnathos arms converge abruptly and the valva is relatively short and truncate.

In the female the genitalia are similar to those of *S. percna*, but in *S. xantharrenes* the underside of the forewing is suffused with fuscous, whereas it is white in *S. percna*.

BIOLOGY. At rest on the stem of *Eleocharis dulcis* (Common, 1960).

DISTRIBUTION. Australia.

MATERIAL EXAMINED

Australia: 1 ♂, 1 ♀, Queensland, 12 mls [19 km] E. of Duaringa, 18.iii.1958 (*Common*) (BMNH) (paratypes).

Scirpophaga melanoclista Meyrick, 1935
(Figs 39, 40, 100, 142, 143, Map 12)

Scirpophaga melanoclista Meyrick, 1935: 553. Holotype ♂, ZAIRE: 'Elisabethville' [Lubumbashi], 31.i.1933 (*Ch. Seydel*), (MRAC, Tervuren) [examined].

♂ (Fig. 142). 23–32 mm. Pale ochreous white. Length of labial palpus approximately 1·4 times diameter of compound eye. Forewing pale ochreous white to pale ochreous, costal margin strongly tinged with dark fuscous, underside fuscous; hindwing white, underside fuscous in costal half.

♀ (Fig. 143). 26–37 mm. White. Fore- and hindwing white on both surfaces, frenulum single-bristled. Anal tuft ochreous yellow.

GENITALIA ♂ (Figs 39, 40). Uncus and gnathos relatively long; gnathos arms converging gradually; subteguminal process flattened, oval-shaped with smooth margin; valva truncate; aedeagus slender, more or less uniform diameter throughout, vesica with coarse spines, one slender cornutus present.

GENITALIA ♀ (Fig. 100). Ostium bursae relatively narrow; ductus bursae narrow, tube-like, without antrum, sclerotized plates between ostium bursae and ductus seminalis U-shaped in cross section; groups of setae always present posterior to ostium bursae.

REMARKS. *S. melanoclista* is the only representative of the *praelata*-group known from Africa. The male can be separated from those of the other white species by the presence of the dark fuscous line along the costa. In the genitalia, the large oval-shaped subteguminal process and the solitary slender cornutus are characteristic. In the female the features distinguishing this species are the tube-like ductus bursae which is more or less uniform in diameter and the presence of the two groups of setae posterior to the ostium bursae (Fig. 100).

BIOLOGY. Unknown.

DISTRIBUTION. Senegal, Sierra Leone, Ghana, Zaire, Angola, Zambia, Madagascar.

MATERIAL EXAMINED

Senegal: 1 ♂, 1 ♀, Kaolack, 1909 (*Melou*) (BMNH). **Sierra Leone**: 1 ♂, Pt Lokko (*Penny*) (BMNH). **Ghana**: 1 ♀, Kete-Krachi (*Cardinall*) (BMNH). **Zaire**: 2 ♂, Lubumbashi (Elisabethville), 25.iii.1934, 4.ii.1935 (BMNH). **Angola**: 1 ♂, Daugo, 31.xii.1912 (MNHN, Paris). **Zambia**: 1 ♀, Lealui, Barotse (*Coryndon*) (BMNH); 1 ♂, Matongo I. nr Lake Bangweulu, 23.xi.1946 (BMNH). **Madagascar**: 2 ♂, 4 ♀, Tananarivo (*Waterlot*) (MNHN, Paris); 1 ♀, 22.xii.1927 (*Decary*) (MNHN, Paris); 4 ♂, 16 ♀, Nanisana nr Tananarivo, xii.1931-i.1932 (*Olsovfieff*) (BMNH); 1 ♀, 19.i.1930 (MNHN, Paris); 1 ♀, no further data (MNHN, Paris).

The *excerptalis*-group

Forewing with vein R_1 anastomosing with *Sc*. Frenulum a single bristle in both sexes.

GENITALIA ♂. Uncus and gnathos moderately long and slender, gnathos arms converging gradually; tegumen with sclerotized thickening somewhat ×-shaped; subteguminal process spine-like (except *S. khasis* which is tuberculiform and is absent in *S. flavidorsalis*); manica with two groups of strong spines (except in *S. xanthogastrella* which is uniformly arranged minute spines); aedeagus slender, more or less uniform in diameter, vesica usually lined with coarse spines.

GENITALIA ♀. Ostium bursae broad, membranous, wrinkled, lined internally with minute spines; ductus bursae membranous; ductus seminalis usually arising from ductus bursae closer to ostium bursae than to corpus bursae; corpus bursae with dense spines.

The *excerptalis*-group consists of 10 species. Five are endemic in Asia: *xanthogastrella*, *magnella*, *brunnealis*, *khasis* and *tongyaii*; three are Australasian: *flavidorsalis*, *melanostigma* and *excerptalis*. The last-mentioned is important because it is a very serious pest of sugar-cane; it has the common name 'top borer' and has been misidentified as '*S. nivella*'. The remaining two species of this group occur in Africa: *ochritinctalis* and *bradleyi*.

Although in the male genitalia of *S. tongyaii* the uncus is rather broad, and in *S. khasis* the subteguminal process is tubercle-like and is absent in *S. flavidorsalis*, the other characters correspond to those of this species-group. Only the female of *S. melanostigma* is known; it shows characters typical of this species-group and it is possible that it is the female of *S. flavidorsalis*. This is discussed under *S. melanostigma*.

Key to species of the *excerptalis*-group

Males

The male of *S. melanostigma* is unknown.

1 Subteguminal process absent, if present tubercle-like 2
– Subteguminal process present, spine-like, except plate-like in *S. bradleyi* 3
2 Tegumen with dorsal sclerotized thickening long, ×-shaped (Fig. 61); manica with two bands of sclerotized plates bearing spines at one end; aedeagus uniform in diameter, vesica with coarse spines (Fig. 62) . . . . **khasis** (p. 230)
– Tegumen with dorsal sclerotized thickening broad, ×-shaped (Fig. 63); manica with two groups of spines; aedeagus expanded at apical end, vesica with flat plate-like, serrated-margined cornutus (Fig. 64) . . . . **flavidorsalis** (p. 230)
3 Subteguminal process plate-like; uncus and gnathos relatively short; tegumen large, strongly bent downwards (Fig. 59) . . . . **bradleyi** (p. 229)
– Subteguminal process spine-like; uncus and gnathos relatively long; tegumen not strongly bent downwards. 4
4 Uncus broad; gnathos arms converging abruptly (Fig. 53) . . . . . **tongyaii** (p. 232)
– Uncus slender; gnathos arms converging gradually (Fig. 27) 5
5 Forewing dull ochreous brown with one dark fuscous spot; subteguminal process a long curved spine (Fig. 55) . . . . **brunnealis** (p. 228)
– Forewing pale ochreous white with or without spot at lower angle of cell; subteguminal process not as above 6
6 Gnathos wrinkled apically; subteguminal process a large spine (Fig. 49); manica with two bands of sclerotized plates bearing spines at one end (Fig. 50) . . . . **excerptalis** (p. 223)
– Gnathos not wrinkled apically; subteguminal process varied; manica with two groups of strong spines or uniformly arranged spines 7

7 Subteguminal process a long, slender, straight spine (Fig. 57) . . . . ***ochritinctalis*** (p. 229)
– Subteguminal process a short, stout spine 8
8 Manica with two groups of strongly sclerotized spines; vesica with coarse spines (Fig. 52) ***magnella*** (p. 226)
– Manica with uniformly arranged spines; vesica with minute spines (Fig. 66) ***xanthogastrella*** (p. 227)

Females

The females of *S. flavidorsalis, S. brunnealis* and *S. khasis* are unknown.

1 African species 2
– Asian or Australian species 3
2 Ostium bursae lined with dense minute spines, especially towards ductus bursae; ductus bursae with section between ostium bursae and ductus seminalis lined with annulated sclerotized plates; apophyses anteriores and apophyses posteriores slender (Fig. 109) . ***ochritinctalis*** (p. 229)
– Ostium bursae lined with few minute spines; ductus bursae with section between ostium bursae and ductus seminalis lined with unannulated sclerotized plates; apophyses anteriores and apophyses posteriores short (Fig. 110) . . . . ***bradleyi*** (p. 229)
3 Ostium bursae strongly wrinkled, lined with dense spines 4
– Ostium bursae slightly wrinkled, lined with less dense spines 5
4 Ostium bursae strongly wrinkled, forming a compact mass (Fig. 105) . . ***excerptalis*** (p. 223)
– Ostium bursae strongly wrinkled, not forming a compact mass (Fig. 106) . . ***magnella*** (p. 226)
5 Forewing always with one dark fuscous spot; labial palpus long with length approximately 4 times diameter of compound eye; apophyses anteriores and apophyses posteriores short (Fig. 108) . . . . ***melanostigma*** (p. 231)
– Forewing without dark fuscous spot; labial palpus with length less than 3 times diameter of compound eye; apophyses anteriores and apophyses posteriores slender 6
6 Ostium bursae lined with minute spines arranged in somewhat circular pattern near ductus bursae; ductus bursae between ostium bursae and ductus seminalis lined with annulated sclerotized plates (Fig. 107) . . . . ***tongyaii*** (p. 232)
– Ostium bursae lined with irregular minute spines; ductus bursae between ostium bursae and ductus seminalis sclerotized and constricted, otherwise membranous, dilated towards corpus bursae (Fig. 111) . . . . ***xanthogastrella*** (p. 227)

Scirpophaga excerptalis (Walker, 1863) **sp. rev.**
(Figs 49, 50, 105, 144, 145, 146, Map 7)

Chilo excerptalis Walker, 1863*a* (April): 142. Holotype ♂, INDIA: 'N. India, 48.131' (BMNH, Pyralidae genitalia slide no. 6319) [examined].

Scirpophaga monostigma Zeller, 1863 (July): 3; Hampson, 1895: 913; 1896: 46 [partim]; de Joannis, 1929: 608. Holotype ♂, locality unknown: 'Coll. H. Sch., Patria Ignota'; 'Coll. Staudinger' (MNHU, Berlin) [examined]. **Syn. n.**

Scirpophaga butyrota Meyrick, 1889: 520. LECTOTYPE ♂, NEW GUINEA: 'Port Moresby, New Guinea, K./88' (BMNH, Pyralidae genitalia slide no. 4021), here designated [examined]. **Syn. n.**

Scirpophaga intacta Snellen, 1890: 94; Hampson, 1895: 913; 1896: 46 [as synonym of *Scirpophaga auriflua* Zeller]; de Joannis, 1929: 608. Lectotype ♂, JAVA: 'Java Tagal, Luc.'; 'Dr. Krüger, Kagok, Tagal, Java, Boorder, Pl. 1, Fig. 3' (RNH, Leiden), designated by Munroe et al. (1958: 77) [examined]. **Syn. n.**

Scirpophaga excerptalis (Walker) Hampson, 1895: 913; Leech, 1901: 402 [partim]; Butani, 1970: 169 [as synonym of *Tryporyza nivella* (F.)].

[*Scirpophaga chrysorrhoa* Zeller sensu Hampson, 1895: 913 [partim]. Misidentification.]

[*Scirpophaga auriflua* Zeller sensu Hampson, 1895: 913; 1896: 46 [partim]; sensu Leech, 1901: 401 [partim]. Misidentifications.]

Topeutis [*sic*] *rhodoproctalis* Hampson, 1919*b*: 319. Holotype ♀, SINGAPORE: Singapore (*H. N. Ridley*) (BMNH, Pyralidae genitalia slide no. 6324) [examined]. **Syn. n.**

[*Scirpophaga xanthogastrella* (Walker) sensu Fletcher & Ghosh, 1920: 381, pl. 41, pl. 42, fig. 1 [partim]. Misidentification.]

[*Scirpophaga nivella* (F.) sensu Shibuya, 1928: 61, pl. 4, fig. 27 [partim]; sensu Moritsuga, 1931: 1–56 [partim]; sensu Jepson, 1954: 9, pl. 1. Misidentifications.]

Tryporyza butyrota (Meyrick) Common, 1960: 340.

[*Tryporyza nivella* (F.) sensu Butani, 1970: 169; sensu Nagaraja, 1972: 507. Misidentifications.]

♂ (Figs 144, 146). 22–28 mm. White. Length of labial palpus approximately 1·5 times diameter of compound eye. Forewing white, sometimes with dark fuscous spot at lower angle of cell, underside pale ochreous; hindwing white.

♀ (Fig. 145). 26–35 mm. White. Fore- and hindwing white; frenulum single-bristled. Anal tuft orange-red (ochreous-yellow in specimens from China, Taiwan, Japan).

GENITALIA ♂ (Figs 49, 50). Uncus moderately long, gnathos slightly wrinkled at apex; subteguminal process a long spine; valva expanded distally; manica with two sclerotized bands, at one end bearing a group of spines; aedeagus slender, vesica with coarse spines.

GENITALIA ♀ (Fig. 105). Ostium bursae broad, wrinkled, strongly sclerotized, lined with spines; ductus bursae membranous; corpus bursae with dense spines.

REMARKS. Meyrick mentioned four specimens from the same locality in the type-series of *S. butyrota*, but only three have been found and examined. One of them, the paralectotype female, is actually *S. nivella*. From the original description, it is evident that Meyrick misidentified the females, since he described the anal tuft as 'whitish-ochreous'. All females of *S. excerptalis* from New Guinea have the anal tufts orange-red.

The male of *S. excerptalis* can be separated from the other white species by the long, spine-like subteguminal process and the two sclerotized bands with spines in the manica. Externally the female can be distinguished from other similar species by having an orange-red anal tuft. However, females from China, Taiwan, Japan and the Solomon Islands have an ochreous-yellow anal tuft, but the structure of the ostium bursae, which is wrinkled, strongly sclerotized, forming a compact mass, and lined with spines, is characteristic.

It is worth noting that most of the females from Taiwan have the sclerotized ostium bursae less wrinkled than in specimens from other localities, while in the males, no differences in the genitalia could be found.

BIOLOGY (for host plants see p. 192). This species had in the past been misidentified as *S. nivella*, as mentioned under that species. *S. excerptalis*, which has the common name 'top borer', is a very serious pest of sugar cane, whereas *S. nivella* is mainly a pest of rice. The host plants of *S. excerptalis* can be found in the references under the name *S. nivella*. Whether there is only one species involved or more than one has to be carefully checked. Moritsugu (1931), cited by Jepson (1954) in his well-known review of the literature, mentioned that apart from sugar-cane, '*S. nivella*' also feeds on *Miscanthus sinensis, Imperata cylindrica*, *Phragmites longivalvis*, *Ischaemum rugosum* and *Typha capensis*. There is reason to believe that there is more than one species involved. (See discussion under *S. nivella*, p. 212.)

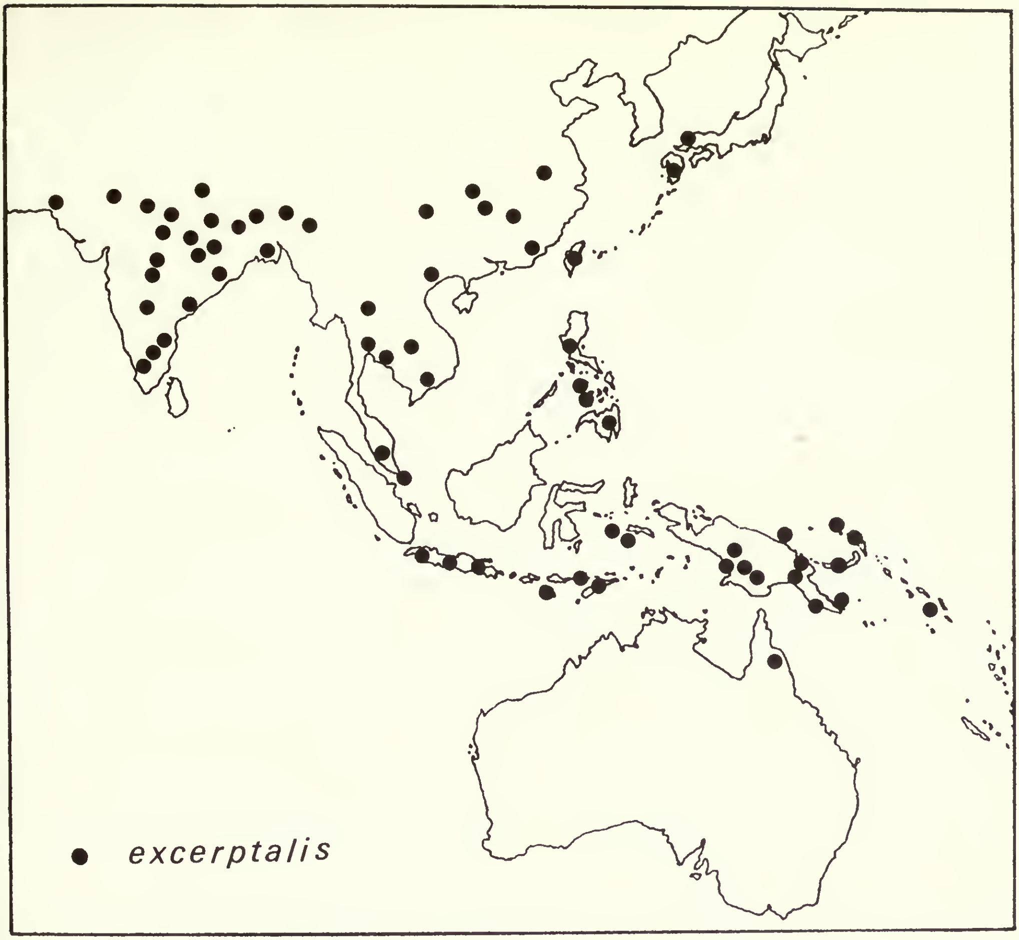
Avasthy (1968) listed the following host plants of the 'top borer' from published references: *Saccharum spontaneum* in India, Indonesia and Pakistan; *Andropogon sorghum, Chloris barbata, Echinochloa colona*, *Pennisetum purpureum*, *Panicum* sp., *Erianthus munja, Sclerostachya fusca* and *Sorghum halepense* in India; *Miscanthus sinensis*, *Ischaemum rugosum*, *Imperata arundinacea* and *Pennisetum typhoideum* in Taiwan; *Oryza sativa* in Indonesia, Japan, Malaysia, Philippines and Thailand. These host plants need to be critically checked and confirmed.

Narayanan & Vankatraman (cited by Butani, 1970) observed that a male of the plain white-winged species known as *S. nivella* bred freely with a female of the spotted-winged species known as *S. monostigma*. As the off-spring consisted of spotted and non-spotted forms, they concluded that in India there is only one species of sugar-cane 'top borer', viz. *S. nivella*. This opinion is supported by Butani (1970).

The most common species of 'top borer' on sugar-cane is *S. excerptalis* in which both sexes can be with or without spots. There is also another species, *S. magnella*, on sugar-cane which is similar externally to *S. excerptalis*. The differences between these two species are evident only in the genitalia. Their distributions partly overlap but *S. magnella* is not as widely distributed as *S. excerptalis*.

The life history of *S. excerptalis* needs to be confirmed.

DISTRIBUTION. Pakistan, India, Nepal, Bangladesh, China, Taiwan, Japan, Thailand, Vietnam, Singapore, West Malaysia, Java, Sumba Island, Timor, Buru Island, Adonara Island, Ambon



Map 7

Island, Philippines, New Guinea, New Hannover, New Britain, New Ireland, Australia, Solomon Islands.

MATERIAL EXAMINED

Pakistan: 1 ♂, Santhoro, on *Saccharum* sp., 7.vi.1964 (BMNH); 1 ♂, 1 ♀, Tandojana, on *Saccharum* sp., 24–25.iv.1965 (BMNH); 1 ♀, Tandojana, 10.vi.1964 (BMNH); 1 ♂, 1 ♀, Lyallpur (BMNH). **India**: 1 ♀, Allahabad (BMNH); 1 ♂, 1 ♀, Bangalore, resting on *Oryza sativa*, 13.x., 19.xi.1962 (BMNH); 1 ♂, 3 ♀, Coimbatore, on *Saccharum* sp., xi.1935, iv., xii.1936 (BMNH); 2 ♂, Dildarnagar, 24.ii.1903 (*Betton*) (BMNH); 1 ♀, Ganjam (BMNH); 1 ♀, Godavari District, Samalkot, at light, xii.1925 (*Rao*) (BMNH); 1 ♀, Bhopal, on *Saccharum* sp., 7.iv.1938 (BMNH); 2 ♂, Kanpur, 5–7.vi.1935 (*Sanders*) (BMNH); 1 ♂, Kanpur, on *Saccharum* sp., 27.iv.1899 (BMNH); 1 ♂, 1 ♀, Karnal, on *Saccharum* sp., 29, 31.vii.1938 (*Ahamad*) (BMNH); 6 ♂, 1 ♀, Mandya, resting on *Oryza sativa*, viii–xi.1962 (BMNH); 1 ♀, Manpur (BMNH); 1 ♂, Moghal Sarai, 28.ii.1903 (*Betton*) (BMNH); 1 ♀, New Delhi, on *Saccharum* sp., 17.iii.1938 (*Dayal*) (BMNH); 1 ♂, Pusa, 7.iii.1930 (*Gupta*) (BMNH); 1 ♂, Pusa, 25.vi.1929 (*Singh*) (BMNH); 1 ♀, Pusa, on *Saccharum* sp., 31.vii.1935 (*Khan*) (BMNH); 1 ♂, Pusa, on *Saccharum* sp., 25.vii.1914 (BMNH); 1 ♂, Pusa, on *Triticum* sp., 1.iii.1913 (BMNH); 1 ♀, Pusa, 9.iii.1928 (*Singh*) (BMNH); 1 ♀, Pusa, on *Saccharum* sp., 27.iv.1933 (*Batra*) (BMNH); 1 ♂, Pusa, 4.iii.1929 (*Hassan*) (BMNH); 1 ♂, 1 ♀, Pusa, on *Saccharum* sp., 16.vi.1932, 25.iii.1935 (BMNH); 1 ♂, Pusa, at light, 6.vii.1926 (BMNH); 1 ♂, Pusa, 10.iii.1928 (*Fletcher*) (BMNH); 1 ♂, Sambalpur, Orissa, resting on *Oryza sativa*, 25.vii.1962 (BMNH); 1 ♂, Tezpur, Assam (BMNH); 2 ♂, 2 ♀, no further data (BMNH); 2 ♂, no further data (*Hearsey*) (UM, Oxford). **Nepal**: 1 ♂, Katmandu, 1400 m, 22.viii.1964 (*Dierl*) (ZSBS, Munich); 1 ♂, 1 ♀, Rapti Tal, Monachari Khola, Belwa, 350 m, 11–12.v.1967 (*Dierl, Forster & Schacht*) (ZSBS, Munich). **Bangladesh**: 1 ♀, Bengal (BMNH). **China**: 1 ♂, Changyang, v.1888 (*Leech*) (BMNH); 1 ♂, Chin-Fu-San (*Maw*) (BMNH); 2 ♂, Hoengshan, Hunan, 4, 15.vi.1933 (*Höne*) (MAK, Bonn); 1 ♂, 1 ♀, Kuatun, Fukien, 2300 m, 13, 20.vi.1933 (*Klapperich*) (BMNH); 1 ♂, Lungtan, nr Nanking, Prov. Kiangsu, 31.v.1933 (*Höne*) (MAK, Bonn); 1 ♂, Siao-lou (BMNH); 5 ♂, 3 ♀, W. China (BMNH). **Taiwan:** 2♀, Banshorio, 24–26.v.1906 (*Wileman*) (BMNH); 35 ♂, 11 ♀, Kanshirei, 4.iv.–14.ix.1906–1909 (*Wileman*) (BMNH); 8 ♂, 3 ♀, Koannania, iv.–viii.1906 (*Wileman*) (BMNH); 30 ♂, 20 ♀, Tainan, on *Saccharum* sp. (*Chen*) (BMNH); 11 ♂, 3 ♀, Wanta nr Hori (Puli), Nan Tou Hsien, 2.iv.–8.v.1966 (CNC, Ottawa); 4 ♂, 2 ♀, 7.v.–23.vi.1906–08 (*Wileman*) (BMNH). **Japan**: 2 ♂, 2 ♀, Satsuma, Kyushu, v.1886 (*Leech Coll.*) (BMNH); 1 ♀, viii.1886 (*Leech Coll.*) (BMNH); 2 ♂, Kyushu, 14.vi., 10.viii.1958 (*Yoshii*) (CNC, Ottawa); 1 ♀, no further data, 1892 (BMNH). **Thailand**: 1 ♂, Bangkok, at light, 17.vi.1951 (*Vorasap*) (BMNH); 2 ♂, 4 ♀, Lampang, on *Saccharum officinarum*, 9–17.viii., 12.xii.1947, 1961 (*Munyeekul*) (DA, Bangkok); 3 ♀, Cholburi, on *Saccharum officinarum*, 25.vii.–4.x.1935 (*Penchitr*) (DA, Bangkok); 1 ♂, Rangsit, 22.vi.1926 (*Ladell*) (BMNH); 1 ♀, Udornthani, on *Saccharum officinarum*, 19.x.1956 (*Maneechote*) (BMNH); 7 ♂, 8 ♀, Udornthani, on *Saccharum officinarum*, 17.viii.–17.x.1954, 1958 (*Munyeekul, Pholboon, Groh*) (DA, Bangkok). **Vietnam**: 1 ♀, Tongking, 9.iii.1916 (MNHN, Paris); 1 ♀, Bin Hoa, xii.1902 (MNHN, Paris). **West Malaysia**: 1 ♂, Kuala Lumpur, 22.iii.1930 (*Corbet*) (BMNH). **Java**: 1 ♂, Besuki, 1891 (*Vaal*) (MNHN, Paris); 1 ♂, Djoenggo Ardjuno, 4500 ft [1360 m], vi.1934 (*Kalis*) (BMNH); 1 ♀, Krakatau, vii.1924 (BMNH). **Sumba Island**: 1 ♂, ii.1896 (*Doherty*) (BMNH). **Timor**: 1 ♀, Dili, v.1892 (*Doherty*) (BMNH); 1 ♀, Suai, 22–31.xii.1912 (*Wahr*) (BMNH). **Buru Island**: 1 ♂, 1922 (*Toxopeus*) (RNH, Leiden). **Adonara Island**: 4 ♂, xi.1891 (*Doherty*) (BMNH). **Ambon Island**: 2 ♂, 1 ♀, no further data (BMNH). **Philippines**: 14 ♂, 8 ♀, Luzon Benquet, Klondyke, 800 ft [240 m], 18.xii.1911–24.v.1912 (*Wileman*) (BMNH); 1 ♂, 2 ♀, Montalban, 25.i.–11.v.1914 (*Wileman*) (BMNH); 2 ♀, Benquet, Palali, 2000 ft [600 m], 28–30.vi.1913 (*Wileman*) (BMNH); 4 ♂, 3 ♀, Mt Makiling, Luzon (NMNH, Washington); 1 ♀, Panay (*Wahr*) (BMNH); 4 ♂, 6 ♀, Victorias occ. Negros, on *Saccharum* sp., v.,x. (*Pierce*) (NMNH, Washington); 2 ♂, Canlubang, 821 m, 26–29.xi.1927 (NMNH, Washington); 1 ♂, 2 ♀, Mindanao, x. (NMNH, Washington); 1 ♂, Los Banos, 14.ii.1922 (*Woodworth*) (NMNH, Washington); 1 ♀, Los Banos, on *Saccharum sponteneum*, 17.ii.1928 (*Fernandez*) (NMNH, Washington). **New Guinea**: 1 ♂, Port Moresby, New Guinea, K./88 (BMNH) (paralectotype of *Scirpophaga butyrota* Meyrick); 4 ♂, 1 ♀, Kumusi R., v.–vii.1907 (*Meek*) (BMNH); 3 ♀, Upper Setekwa R., Snow Mts, 2000–3000 ft [600–910 m], viii.1910 (*Meek*) (BMNH); 1 ♀, Mt Goliath, 5000–7000 ft [1500–2100 m], ii.1911 (*Meek*) (BMNH); 1 ♀, Astrolabe Bay, vii. (*Wahnes*) (BMNH); 2 ♂, 1 ♀, Wataikwa R., viii., x.1910 (*Wollaston*) (BMNH); 3 ♂, 1 ♀, Ninay Valley, 3500 ft [1060 m], ii., iii.1909 (BMNH); 2 ♀, Utakwa R., xii.1912, i.1913 (*Wollaston*) (BMNH); 2 ♀, Mt Hagen, on *Saccharum robustum*, ii.1964 (*Simmonds*) (BMNH); 5 ♂, 3 ♀, Dampier Is., ii., iii.1914 (*Meek*) (BMNH); 1 ♂, Haidana, Collingwood Bay, iv.1907 (*Meek*) (BMNH); 1 ♂, Milene Bay, xi.1898 (*Meek*) (BMNH); 2 ♂, Aiyura, 6000 ft [1820 m], 27.ix.1957 (*Munroe & Holland*) (CNC, Ottawa); 3 ♂, Padwe, Sepik R., 26.x.1957 (*Munroe & Holland*) (CNC, Ottawa); 1 ♂, Lae, 30.viii.1957 (*Munroe & Holland*) (CNC, Ottawa); 1 ♂, Koigin, 1200 ft [360 m], 22.x.1957 (*Munroe & Holland*) (CNC, Ottawa); 4 ♂, 3 ♀, Boroko, nr Port Moresby, 300 ft [90 m], 19.viii.1957 (*Munroe & Holland*) (CNC, Ottawa); 1 ♂, Brown R., Karema, 20.viii.1957 (*Munroe & Holland*) (CNC, Ottawa); 1 ♀, Kokoda, 1200 ft [360 m], x.1933 (*Cheesman*) (BMNH); 5 ♂, 1 ♀, Vulcan I., xi.1913–i.1914 (*Meek*) (BMNH); 6 ♂, 2 ♀, Fergusson I., ix.1894 (*Meek*) (BMNH); 1 ♀, Fergusson I., xii.1895 (BMNH); 1 ♂, Fergusson I., Deidei, Comwa Bay (BMNH); 1 ♂, 2–6.vii.1956 (*Brass*) (BMNH); 1 ♀, Long I., 24–27.v.1932 (BMNH). **New Hannover**: 1 ♂, iii.1923 (*Meek*) (BMNH). **New Britain**: 1 ♂, 2 ♀, i.–ii.1925 (*Eichhorn*) (BMNH). **New Ireland**: 2 ♂, xi, xii.1923 (*Eichhorn*) (BMNH). **Australia**: 1 ♀, Kuranda, Queensland, x.1919 (*Dodd & Sons*) (BMNH). **Solomon Islands**: 3 ♀, Guadalcanal I., Honiara, 8–18.xi.1953 (*Bradley*) (BMNH).

Scirpophaga magnella de Joannis, 1929

(Figs 51, 52, 106, 147, 148, 149, Map 6)

Scirpophaga magnella de Joannis, 1929: 608. Holotype ♀, VIETNAM: 'Choganh [Tongking], vi., 1920–1932, Coll. L. & J. de Joannis' (MNHN, Paris) [examined].
[*Scirpophaga monostigma* Zeller sensu Hampson, 1895: 913; 1896: 46 [partim]. Misidentification.]
[*Scirpophaga auriflua* Zeller sensu Leech, 1901: 401 [partim]. Misidentification.]

♂ (Fig. 148). 25–40 mm. External characters as in *S. excerptalis*.

♀ (Figs 147, 149). 32–49 mm. External characters as in *S. excerptalis* but sometimes forewing with one dark fuscous spot at lower angle of cell. Anal tuft always ochreous-yellow.

GENITALIA ♂ (Figs 51, 52). Uncus and gnathos slightly bent downwards; tegumen with dorsal sclerotized thickening X-shaped, sometimes the lower part weak, resulting in a more or less Y-shaped structure;

subteguminal process stout, spine-like, valva with apex more or less pointed; manica with two groups of spines; aedeagus slender, vesica with coarse spines.

GENITALIA ♀ (Fig. 106). Ostium bursae broad, wrinkled, lined with spines; ductus bursae membranous, section between ostium bursae and ductus seminalis with a strong sclerotized plate.

REMARKS. *S. magnella* is very similar externally to *S. excerptalis* with which it is partially sympatric. The males are best separated from the latter by the difference in the shape of the subteguminal process of the genitalia. In *S. magnella* the process is in the form of a stout short spine, while in *S. excerptalis* it is a more slender long spine. The female of these two species can be distinguished by the colour of the anal tuft, which is usually orange-red in *S. excerptalis* and ochreous-yellow in *S. magnella*. Furthermore, in the genitalia the ostium bursae of *S. excerptalis* is strongly wrinkled and sclerotized, while in *S. magnella* it is less wrinkled.

BIOLOGY (for host plants see p. 192). The life history of this species is not known for certain; it has probably been confused with *S. excerptalis* and studied under the name *S. nivella*.

DISTRIBUTION. Iran, Afghanistan, Pakistan, India, Nepal, Bangladesh, Burma, Thailand, Vietnam, China, Hong Kong.

MATERIAL EXAMINED

Iran: 2 ♂, Baluchistan, Anfang, Tahte-Malek, 750 m, v. 1938 (*Brandt*) (LN, Karlsruhe). **Afghanistan**: 1 ♂, Sarobi, 1100m, 2.vi.1961 (*Ebert*) (ZSBS, Munich); 1 ♀, Barikot, Nuristan, 1800 m, 12–17.vii.1963 (*Kasy & Vartian*) (NM, Vienna). **Pakistan**: 1 ♂, Campbellpore (BMNH); 1 ♀, Campbellpore, 28,viii.1885 (BMNH); 1 ♀, Rawalpindi, on *Saccharum bengalense,* 7.xii.1960 (BMNH); 1 ♂, Lahore (BMNH). **India:** 1 ♂, Chausa, 17.iii.1904 (*Betton*) (BMNH); 1 ♂, 1 ♀, Dharmsala (BMNH); 1 ♂, Kanpur [Cawnpore], 20.iii.1905 (*Betton*) (BMNH); 1 ♀, Kapurthala, Punjab, resting on *Oryza sativa,* ix.1962 (BMNH); 2 ♂, 1 ♀, Manpur (BMNH); 1 ♂, Margarita, Upper Assam, v.1889 (*Doherty*) (BMNH); 1 ♂, 1 ♀, Mughal Sarai, 10.iii.1904 (*Betton*) (BMNH), 1 ♂, Punjab, vii.1886 (BMNH); 1 ♂, Pusa, at light, 27.v.1932 (BMNH); 1 ♀, Roorkee, 30.vi.1934 (*Graham*) (BMNH); 1 ♀, Sandi, iii.1880 (BMNH); 1 ♂, Montrpur, on *Erianthus munja,* iii.1971 (BMNH); 2 ♂, 3 ♀, NW. India (BMNH); 4 ♂, no further data (BMNH); 1 ♀, no further data (*Hearsey*) (UM, Oxford). **Nepal**: 1 ♂, Barang (BMNH); 2 ♂, 1 ♀, Rapti Tal 300 m, 23.iii.–4.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich). **Bangladesh**: 1 ♂, 1 ♀, Furshedpur, on *Saccharum* sp., 23.vii.1968 (BMNH); 1 ♂, Chandkhir, Sylhet (BMNH); 1 ♀, Kushtia, on *Saccharum* sp. (BMNH); 1 ♀, Bengal (BMNH). **Burma**: 1 ♂, Rangoon (BMNH). **Thailand**: 1 ♀, Chiangmai, 1000 ft [300 m], 8.v.1939 (*Tongyai*) (DA, Bangkok). **Vietnam**: 1 ♂, Cha Pa, Tongking, ii.1929 (MNHN, Paris); 1 ♂, Ngan-Son, Tongking (BMNH); 1 ♀, Tongking (*Cooman*) (MNHN, Paris. **China**: ♂, Hainan, vi.1906 (BMNH); 1 ♂, Ichang, vi.1888 (BMNH); 1 ♂, 1 ♀, no further data (BMNH). **Hong Kong**: 1 ♀, v.1892 (BMNH).

Scirpophaga xanthogastrella (Walker, 1863)
(Figs 65, 66, 111, 150, 151, Map 4)

Apurima xanthogastrella Walker, 1863*a*: 194; Moore, 1867: 666; 1886: 388, pl. 184, fig. 14; Hampson, 1895: 913; 1896: 46 [as synonym of *Scirpophaga auriflua* Zeller]; Aurivillius, 1898: 169 [as synonym of *Crambus nivella* F.]; Shibuya, 1928: 61 [as synonym of *Scirpophaga nivella* (F.)]; Butani, 1970: 169. Holotype ♀ [not ♂ as stated by Walker], INDIA: 'S. Ind 61.20' (BMNH, Pyralidae genitalia slide no. 6318) [examined].

Apurima costalis Moore, 1886: 388, pl. 184, fig. 15. Holotype ♂, SRI LANKA: 'Moore Coll. 94.106' (BMNH, Pyralidae genitalia slide no. 6342) [examined]. **Syn. n.**

Schoenobius xanthogastrella (Walker) Hampson, 1893: 46.

Schoenobius costalis (Moore) Hampson, 1893: 46; 1895: 917; 1896: 49.

Scirpophaga xanthogastrella (Walker) Meyrick, 1894: 11; Fletcher, 1928: 58 [as synonym of *Scirpophaga nivella* (F.)].

♂ (Fig. 150). 22–30 mm. Pale ochreous white. Length of labial palpus approximately 2·5 times diameter of compound eye. Forewing pale ochreous white, underside fuscous; hindwing pale ochreous white, underside with fuscous suffusion in costal half.

♀ (Fig. 151). 27–36 mm. White. Fore- and hindwing white on both surfaces; frenulum single-bristled. Anal tuft ochreous yellow.

Genitalia ♂ (Figs 65, 66). Tegumen with dorsal sclerotized thickening X-shaped, subteguminal process small, spine-like; manica with uniformly arranged minute spines; aedeagus with minute spines on vesica.

Genitalia ♀ (Fig. 111). Ostium bursae broad, membranous, slightly wrinkled, with minute spines denser towards ductus bursae; ductus bursae membranous, gradually dilated towards corpus bursae, section between ostium bursae and ductus seminalis constricted, lined with sclerotized plate; corpus bursae with dense spines.

Remarks. This species can be separated from the other white species in this group by the long labial palpus in both sexes, the small spine-like subteguminal process in the male genitalia, and the gradual dilation of the membranous ductus bursae towards the corpus bursae in the female genitalia.

Biology. Fletcher & Ghosh (1920) studied the life cycle of an Indian species which they probably misidentified as *S. xanthogastrella*. The host plants recorded were sugar-cane, kanra (*Saccharum arundinaceum*) and batri (*Saccharum spontaneum*). From the same batch of pupae the adults emerged in two forms, with and without a spot on the forewing. The form with a spot was identified as *Scirpophaga monostigma* Zeller, and the one without a spot as *Scirpophaga xanthogastrella* (Walker). Also from the illustrations (pl. 41, figs 10, 12) there were two female forms, one with a yellow anal tuft, the other orange-red. These differences suggest misidentification. The form with the orange-red anal tuft was certainly *Scirpophaga excerptalis* (Walker) which in both sexes can be with or without a spot on the forewing. The other form, in which the female has the anal tuft yellow, is difficult to identify positively but is most likely *Scirpophaga magnella* de Joannis. This species is also a pest of sugar-cane and the adult has two forms; it is partially sympatric with *S. excerptalis*. The morphology of *S. excerptalis* and *S. magnella* is very similar.

Distribution. Sri Lanka, India, Nepal, Taiwan, Philippines.

Material examined

Sri Lanka: 1 ♂, Galboda, iv.1904 (BMNH); 1 ♂, 1 ♀, Galboda (BMNH); 2 ♀, Pundaloya, iii.1897 (BMNH); 3 ♂, 7 ♀, Pundaloya (BMNH); 9 ♂, 7 ♀, no further data (BMNH). **India**: 1 ♀, Travancore (BMNH); 1 ♀, Alumihare, 6.v.1885 (NMNH, Washington). **Nepal**: 1 ♂, Chisapani Garhi, 1600 m, 11–15.vii.1967 (*Dierl & Schacht*) (ZSBS, Munich); 1 ♀, Likhu Khola Tal, 1700 m, 4.vi.1962 (*Ebert & Falkner*) (ZSBS, Munich). **Taiwan**: 1 ♂, Banshorio, 26.v.1906 (*Wileman*) (BMNH); 1 ♂, 1 ♀, Kanshirei, 27.iv., 25.v.1908 (*Wileman*) (BMNH). **Philippines**: 1 ♂, Klondyke Bonquet, Luzon, 9.v.1912 (*Wileman*) (BMNH); 1 ♀, Baquio, 17.v.1907 (*Betton*) (BMNH).

Scirpophaga brunnealis (Hampson, 1919) **comb. n.**
(Figs 55, 56, 152, Map 5)

Topeutis [*sic*] *brunnealis* Hampson, 1919*b*: 319. Holotype ♂, Burma: 'Up. Chindwisi Dist. [Upper Chindwin District], 96–140' (BMNH, Pyralidae genitalia slide no. 13470) [examined].

♂ (Fig. 152). 27–29 mm. Ochreous brown. Length of labial palpus approximately 3 times diameter of compound eye. Forewing dull ochreous brown, one dark fuscous spot at lower angle of cell, underside fuscous; hindwing ochreous brown on both surfaces.

♀ Unknown.

Genitalia ♂ (Figs 55, 56). Uncus and gnathos relatively long; subteguminal process slender, spine-like; valva broad, expanded distally; manica with two groups of spines; aedeagus slender; vesica with coarse spines.

Remarks. The dull ochreous brown forewing with a dark spot separates *S. brunnealis* from other species of this group. In the genitalia, the slender uncus and gnathos, together with the broad valva and the shape of the subteguminal process, are characteristic.

Biology. Unknown.

Distribution. Burma, Nepal.

MATERIAL EXAMINED

Burma: 1 ♂, Upper Chindwin District (BMNH); 1 ♂, Katha (BMNH). **Nepal**: 1 ♂, Rapti Tal, 20 mls [39 km] W. Hitora, 300 m, 23–27.iii.1962 (*Ebert & Falkner*) (ZSBS, Munich).

Scirpophaga ochritinctalis (Hampson, 1919) comb. n.

(Figs 57, 58, 109, 154, 155, Map 13)

Schoenobius ochritinctalis Hampson, 1919*b*: 323. Holotype ♂, SIERRA LEONE: S. Leone, 19.iv.1875 (*Clements*) (BMNH, Pyralidae genitalia slide no. 6341) [examined].

Scirpophaga macrostoma Meyrick, 1933: 377. LECTOTYPE ♀, ZAIRE: Luebo, xi.1931 (*J. P. Colin*) (MRAC, Tervuren), here designated [examined]. **Syn. n.**

Schoenobius macrostomus (Meyrick) Meyrick, 1935: 554.

♂ (Fig. 154). 24–31 mm. White. Length of labial palpus approximately 2·5 times diameter of compound eye. Forewing pale ochreous-white, underside fuscous; hindwing white, underside suffused with fuscous in costal half.

♀ (Fig. 155). 27–39 mm. White. Forewing very pale yellowish white, underside white; hindwing white; frenulum single-bristled. Anal tuft ochreous yellow.

GENITALIA ♂ (Figs 57, 58). Subteguminal process straight, spine-like; valva truncate distally, costal and ventral margins more or less parallel; aedeagus slender, vesica with coarse spines.

GENITALIA ♀ (Fig. 109). Ostium bursae broad, membranous, cup-shaped, lined with minute spines, especially towards ductus bursae; ductus bursae membranous, section between ostium bursae and ductus seminalis lined with annulated sclerotized plates.

REMARKS. This species can be distinguished from the other white species by the genital structures. In the male, the subteguminal process is a straight spine. In the female, the ostium bursae is cup-shaped and the sclerotized part between the ostium bursae and the ductus seminalis is annulated.

BIOLOGY. Unknown.

DISTRIBUTION. Sierra Leone, Ghana, Nigeria, Central African Republic, Zaire, Uganda, Tanzania, Malawi, Zambia, Angola.

MATERIAL EXAMINED

Ghana: 1 ♀, Achimota, 3.v.1959 (*Morton*) (BMNH); 4 ♀, Kete-Krachi (*Cardinall*) (BMNH). **Nigeria**: 1 ♀, Abinsi, Benue R., 6.xii.1912 (BMNH); 2 ♀, Lagos (BMNH). **Central African Republic**: 4 ♀, Fort Crampel (MNHN, Paris). **Zaire**: 1 ♂, 2 ♀, Arebe, ii (BMNH); 1 ♂, Kadjudju (MNHN, Paris); 1 ♂, Matadi, xi.1931 (MNHN, Paris); 1 ♂, Sankuru, Katako-Kombe, 13.xi.1952 (*Fontaine*) (MRAC, Tervuren). **Uganda**: 4 ♂, 1 ♀, Banda, 26.ii, 13.iii.1899 (*Ansorge*) (BMNH); 1 ♂, 2 ♀, Buekulla, 1899 (*Ansorge*) (BMNH); 1 ♂, Mondo, 11.iii.1899 (*Ansorge*) (BMNH); 3 ♀, Usoga, Mlamba, 4.iii.1899 (*Ansorge*) (BMNH); 5 ♂, Kampala, 10–22.iii.1897, 1899 (*Ansorge*) (BMNH); 1 ♀, Kampala, iii.1900 (*Rattray*) (BMNH); 2 ♀, Kasoha, Unyoro, 11, 25.viii.1897 (*Ansorge*) (BMNH); 2 ♀, Monyonya, Unyoro, 18.iii.1897 (*Ansorge*) (BMNH); 3 ♂, Kilwalogomma (*Ansorge*) (BMNH). **Tanzania**: 1 ♂, 1 ♀, Mpembene, 3760 ft [1140 m], 15.x.1947 (BMNH); 1 ♀, Rukuba Hill, 37 mls [59 km] W. of Nyanza, at light, 7.xi.1915 (*Carpenter*) (BMNH). **Malawi**: 6 ♂, 3 ♀, Mt Mlanje, Luchenya R., 28.x.1913–5.i.1914 (*Neave*) (BMNH); 1 ♂, Ruo Valley, 200 ft [60 m], 16.xii.1913 (*Neave*) (BMNH). **Zambia**: 1 ♂, Lake Bangweulu nr Monfuli, 2.x.1946 (BMNH); 1 ♀, Mpeika, xi.1930 (*Kettlewell*) (BMNH). **Angola**: 1 ♂, Fort Don Carlos, 21.ix.1903 (*Ansorge*) (BMNH).

Scirpophaga bradleyi sp. n.

(Figs 59, 60, 110, 156, 157, Map 13)

♂ (Fig. 156). 37 mm. Pale ochreous. Length of labial palpus approximately 2·8 times diameter of compound eye. Forewing pale ochreous, underside fuscous; hindwing pale ochreous, costal half suffused with pale ochreous on upperside, fuscous on underside.

♀ (Fig. 157). 37 mm. White. Fore- and hindwing suffused with very pale ochreous; frenulum single-bristled. Anal tuft pale ochreous.

GENITALIA ♂ (Figs 59, 60). Uncus and gnathos relatively short; tegumen large, dorsal sclerotized thickening X-shaped; subteguminal process long, plate-like; aedeagus slender; manica with two groups of spines; vesica with coarse spines.

Genitalia ♀ (Fig. 110). Ostium bursae broad, membranous, lined with minute spines, denser towards ductus bursae; ductus bursae membranous, section between ostium bursae and corpus bursae sclerotized; corpus bursae with dense spines; apophyses anteriores and apophyses posteriores short.

Remarks. This species is similar to *S. ochritinctalis* in general appearance. It can be distinguished from the latter by the structure of the genitalia. In the male of *S. bradleyi,* the relatively short uncus and gnathos, the broad tegumen and especially the long plate-like shape of the subteguminal process enable it to be separated from other species in the group. In the female of *S. bradleyi* the ostium bursae, close to the ductus bursae, is lined with less dense spines than in *S. ochritinctalis*. In addition the sclerotized section of the ductus bursae between the ostium bursae and the ductus seminalis is not annulated as it is in *S. ochritinctalis*. The apophyses anteriores and posteriores are also short in *S. bradleyi.*

Biology. Unknown.

Distribution. Angola.

Material examined

Holotype ♂, **Angola**: Fort Don Carlos, 21.ix.1903 (*Dr Ansorge*) (BMNH, Pyralidae genitalia slide no. 11013).

Paratype. 1 ♀, same data as holotype but 22.ix.1903 (BMNH, Pyralidae slide no. 11014).

This species is named after Dr J. D. Bradley, Commonwealth Institute of Entomology, London.

Scirpophaga khasis sp. n.
(Figs 61, 62, 153, Map 4)

♂ (Fig. 153). 26–33 mm. Head pale ochreous white. Length of labial palpus approximately 2 times diameter of compound eye. Forewing shining pale ochreous white with dark fuscous spot at lower angle of cell, underside fuscous; hindwing pale ochreous white, underside fuscous in costal half.

♀. Unknown.

Genitalia ♂ (Figs 61, 62). Uncus and gnathos relatively long, slender; subteguminal process sclerotized, tuberculiform; valva broad distally; manica with two bands of sclerotized plates bearing spines at one end; aedeagus slender, vesica with coarse spines.

Remarks. This species can be very similar to some specimens of *S. excerptalis* and *S. magnella* in which the forewing has a dark fuscous spot at the lower angle of the cell, but the wings of *S. khasis* are more shining. In the genitalia, the tuberculiform nature of the subteguminal process, together with the two bands of sclerotized plates bearing spines at one end and the coarse spines in the vesica, are characteristic of this species.

Biology. Unknown.

Distribution. India.

Material examined

Holotype ♂, **India**: Khasis [Khasi Hills, 25°30′N, 91°30′E], Paravicini Coll. (BMNH, Pyralidae genitalia slide no. 13448).

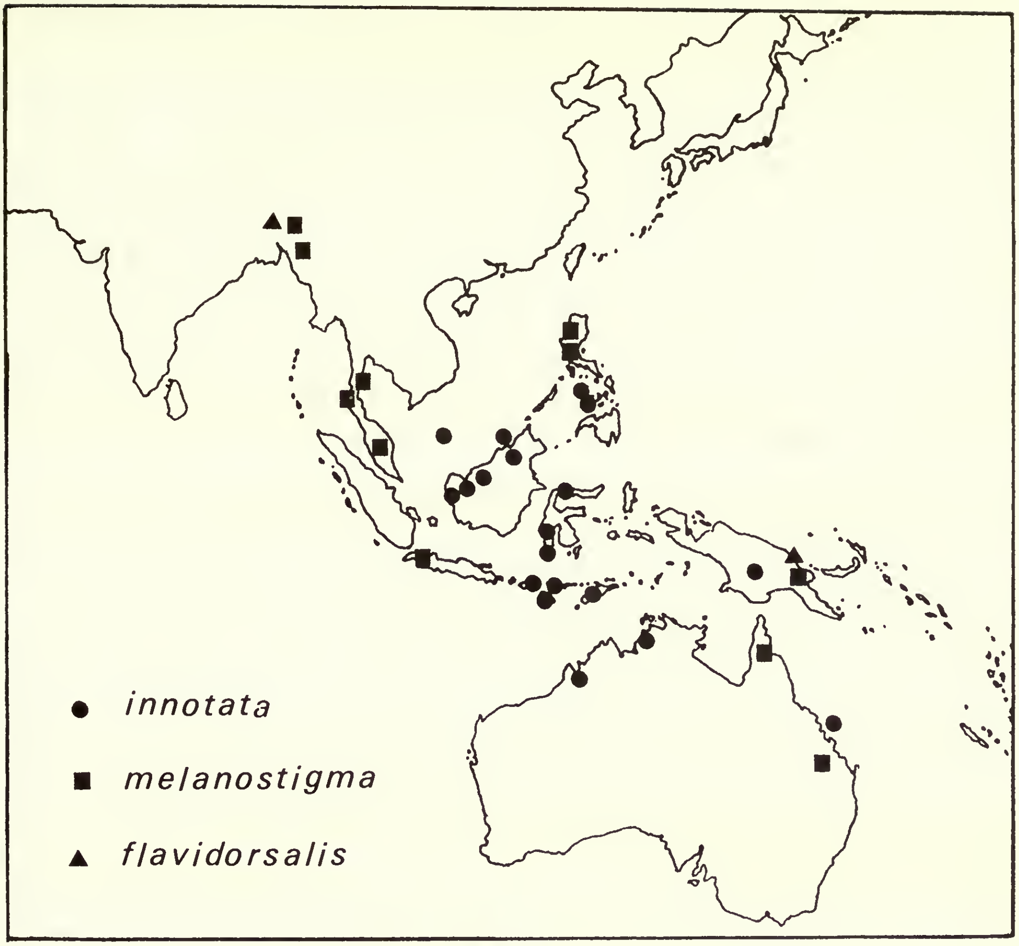
Paratypes. **India**: 10 ♂, same data as holotype; 1 ♂, Khasis, 16.v.1894; 5 ♂, Khasis, iv.1894; 7 ♂, Khasis (all BMNH); 2 ♂, Khasis (UM, Oxford).

Scirpophaga flavidorsalis (Hampson, 1919) **comb. n.**
(Figs 63, 64, 158, Map 8)

Topeutis [*sic*] *flavidorsalis* Hampson, 1919*b*: 319. Holotype ♂, Bhutan: 2.vii.1855 (*Dudgeon*) (BMNH, Pyralidae genitalia slide no. 6325) [examined].

♂ (Fig. 158). 18–28 mm. Pale ochreous white. Labial palpi with spreading scales, in length approximately 3 times diameter of compound eye. Forewing pale ochreous with dark fuscous spot at the lower angle of cell, underside fuscous; hindwing pale ochreous, underside fuscous in costal half.

♀. Unknown.



Map 8

GENITALIA ♂ (Figs 63, 64). Tegumen with dorsal sclerotized thickening X-shaped; subteguminal process tubercle-like, valva relatively short; manica with two groups of spines; aedeagus expanded at distal end, cornutus a flat plate with serrated margin.

REMARKS. Only two males are known; although the specimen from New Guinea is much smaller than the holotype, no differences in the genitalia could be found.

BIOLOGY. Unknown.

DISTRIBUTION. Bhutan, New Guinea.

MATERIAL EXAMINED

New Guinea: 1 ♂, Astrolabe Bay (*Wahnes*) (BMNH).

Scirpophaga melanostigma (Turner, 1922) **comb. n.**

(Figs 108, 159, Map 8)

Schoenobius melanostigmus Turner, 1922: 47. Holotype ♀ [not ♂ as stated by Turner (Common, 1960)], AUSTRALIA: Queensland, Claudie R., 1914 (*J.A.K.*) (NMV, Melbourne) [not examined].
Tryporyza melanostigma (Turner) Common, 1960: 342, fig. 8G, pl. 2, fig. 3.

♂. Unknown.

♀ (Fig. 159). 23–26 mm. White. Labial palpus with spreading scales, in length approximately 4 times diameter of compound eye. Forewing white, gradually changing to pale ochreous towards apex, one dark fuscous spot at the lower angle of the cell; hindwing white; frenulum single-bristled. Anal tuft pale ochreous white.

Genitalia ♀ (Fig. 108). Ostium bursae broad, membranous, lined with minute spines, weakly sclerotized towards ductus bursae; ductus bursae membranous; ductus seminalis arising from ductus bursae near ostium bursae; corpus bursae lined with dense spines.

Remarks. There is some evidence that *S. flavidorsalis* (known from the male only) and *S. melanostigma* (known from the female only) may be opposite sexes of the same species. A male without the abdomen in the NMNH, Washington has the same label data as a female of *S. melanostigma* from Trang, Thailand, and these two specimens are externally very similar.

In the BMNH there are a male of *S. flavidorsalis* and a female of *S. melanostigma* from New Guinea with identical data.

This species can be recognized externally by having a long labial palpus with spreading scales and a dark fuscous spot on the forewing.

Biology. Unknown.

Distribution. India, Bangladesh, Thailand, West Malaysia, Java, Philippines, New Guinea, Australia.

Material examined

India: 1 ♀, Brahmaputra, 27.v.1961 (*Scherer*) (ZSBS, Munich). **Bangladesh**: 1 ♀, Chittagong (BMNH). **Thailand**: 1 ♀, Trang (*Abbott*) (NMNH, Washington); 1 ♀, Chumporn, 12.v.1956 (*Pholboon*) (DA, Bangkok). **West Malaysia**: 1 ♀, Kuala Lumpur, at light, 18.viii.1941 (BMNH); 3 ♀, Kuala Lumpur, at light, 5–6.ii., 25–26.iii.1924 (BMNH). **Java**: 4 ♀, Radjamandala, 350 m, xii.1940 (*Olthof*) (RNH, Leiden). **Philippines**: 3 ♀, Palali, 2000 ft [600 m], 28.vi.–1.vii.1913 (*Wileman*) (BMNH); 1 ♀, Klondyke, 4.vi.1913 (*Wileman*) (BMNH); 1 ♀, Mt Makiling, Luzon (*Baker*) (NMNH, Washington). **New Guinea**: 1 ♀, Astrolabe Bay (*Wahnes*) (BMNH). **Australia**: 1 ♀, Queensland, Claudie R., 20.ii.1914 (*Kershaw*) (ANIC, Canberra) (paratype of *Schoenobius melanostigmus* Turner); 1 ♀, Iron Range, Queensland, 15.iv.1964 (*Common & Upton*) (BMNH).

***Scirpophaga tongyaii* sp. n.**

(Figs 53, 54, 107, 160, 161, Map 5)

♂ (Fig. 160). 25–29 mm. Pale ochreous white. Length of labial palpus approximately twice diameter of compound eye. Forewing pale ochreous white, underside fuscous; hindwing pale ochreous white with fuscous suffusion in costal third.

♀ (Fig. 161). 31–39 mm. White. Fore- and hindwing white on both surfaces; frenulum single-bristled. Anal tuft ochreous yellow.

Genitalia ♂ (Figs 53, 54). Uncus broad; gnathos slender, curved towards uncus; tegumen with dorsal sclerotized thickening in two lines with a tendency to join, forming an X-shaped structure; subteguminal process spine-like; valva with apex pointed posteriorly; manica with two groups of spines; aedeagus slender, vesica with coarse spines.

Genitalia ♀ (Fig. 107). Ostium broad, membranous, lined with spines towards ductus bursae; ductus bursae membranous, section between ostium bursae and ductus seminalis lined with sclerotized annulations; corpus bursae with dense spines.

Remarks. This species can be distinguished from the other white species by genitalic structures in both sexes. In the male the uncus is broad and the gnathos is slender, quite distinct from other species. The dorsal sclerotized thickening of the tegumen in the holotype consists of two narrowly separated lines. In some specimens these lines tend to converge in the middle to form a more or less X-shaped structure. The female genitalia are very similar to those of *S. bradleyi* but the sclerotized part between the ostium bursae and the ductus seminalis of *S. tongyaii* is annulated as in *S. ochritinctalis*. The arrangement of the spines in the ostium bursae of *S. tongyaii* and *S. ochritinctalis* is quite different. Furthermore *S. bradleyi* and *S. ochritinctalis* are known only from Africa while *S. tongyaii* is from Asia.

Biology. Unknown.

DISTRIBUTION. Thailand, Burma, India.

MATERIAL EXAMINED

Holotype ♂, **Thailand**: Kaochong, Trang [7°35′N, 99°35′E], 1–18.iv.1960 (*P. Pholboon*) (DA, Bangkok, Pyralidae genitalia slide no. 114).

Paratypes. **Thailand**: 2 ♀, same data as holotype (DA, Bangkok); 1 ♂, 1 ♀, same data as holotype, but 15.iv.1960 (BMNH); 1 ♂, 1 ♀, same data (DA, Bangkok); 2 ♂, 4 ♀, Trong [Trang], (*Abbott*) (NMNH, Washington).

Non-paratypic material. **Thailand**: 1 ♀, Krabi, 7–25.iv.1962 (*Friedel*) (ZSBS, Munich). **Burma**: 1 ♂, Hkamkawn, 4000 ft [1210 m] (*Swann*) (BMNH). **India**: 2 ♂, Kangra Valley, 4500 ft [1360 m], vii.1899 (*Dudgeon*) (BMNH); 1 ♂, Khasi Hills, Shillong, 5000 ft [1510 m], 12.vi.1923 (*Fletcher*) (BMNH).

This species is named after Dr M. R. Chakratong Tongyai, the Minister of Agriculture, Thailand (at the time of this study) who has made great contributions to entomology, especially in the field of insect taxonomy in Thailand.

The *occidentella*-group

Forewing with vein R_1 usually not anastomosing with *Sc*. Frenulum in male a single bristle, in female with single or double bristle.

GENITALIA ♂. Uncus and gnathos slender, gnathos arms usually converging abruptly, curved towards uncus; tegumen with dorsal sclerotized thickening long, ×-shaped; subteguminal process lobe-like; anellus with dense, strongly sclerotized spines; manica with uniformly arranged minute spines; aedeagus slender, vesica with minute spines.

GENITALIA ♀. Ostium bursae relatively broad, membranous, lined with minute spines; ductus bursae menbranous; ductus seminalis originating from ostium bursae at same level as ductus bursae, this area lined with sclerotized plates; corpus bursae membranous or with spines.

The *occidentella*-group consists of eight species. Five are endemic in Africa: *S. occidentella*, *S. subumbrosa*, *S. marginepunctella*, *S. serena* and *S. goliath*; two in Asia: *S. virginia* and *S. fusciflua*; and one in New Guinea and Australia, *S. ochroleuca*.

Key to species of the *occidentella*-group

Males

The male of *S. goliath* is unknown.

1 Forewing ochreous with markings 2
– Forewing ochreous or ochreous white, without markings 3
2 Anellus with dense strong spines; subteguminal process bilobed; valva broad (Fig. 79) **marginepunctella** (p. 238)
– Anellus with strong spines laterally; subteguminal process single-lobed; valva narrow (Fig. 81) **serena** (p. 239)
3 Anellus with dense strong spines; subteguminal process bilobed (Fig. 77) . **subumbrosa** (p. 237)
– Anellus with strong spines laterally; subteguminal process varied 4
4 Uncus broad, tapering, constricted abruptly near apex; subteguminal process large, bilobed (Fig. 69) . . . . . . **occidentella** (p. 234)
– Uncus slender, tapering towards apex; subteguminal process not large 5
5 Subteguminal process rounded (Fig. 75). . . . . . **virginia** (p. 236)
– Subteguminal process bilobed or slightly bilobed 6
6 Forewing ochreous; gnathos long; subteguminal process slightly bilobed (Fig. 73) **ochroleuca** (p. 235)
– Forewing pale ochreous white; gnathos relatively short; subteguminal process strongly bilobed (Fig. 71) . . . . . . **fusciflua** (p. 234)

Females

1 Frenulum double 2
– Frenulum single 5
2 Corpus bursae with dense spines (Fig. 117) . . . . . . **subumbrosa** (p. 237)
– Corpus bursae membranous or with very few spines 3
3 Corpus bursae with very few spines; ostium bursae without longitudinal wrinkles towards ductus bursae (Fig. 118) . . . . . . **marginepunctella** (p. 238)

– Corpus bursae membranous, without spines; ostium bursae with longitudinal wrinkles towards ductus bursae (Figs 119, 120) 4

4 Forewing ochreous, costal area with pale ochreous white suffusion from base to apex of vein R_2 **serena** (p. 239)

– Forewing fuscous; costal area with pale ochreous white suffusion from base to apex of vein R_3 **goliath** (p. 239)

5 African species . . . . **occidentella** (p. 234)

– Asian or Australian species . . . . **fusciflua** (p. 234), **ochroleuca** (p. 235), **virginia** (p. 236)

Scirpophaga occidentella (Walker, 1863)
(Figs 69, 70, 113, 162, 163, Map 14)

Rupela occidentella Walker, 1863*b*: 524. Holotype ♀ [not ♂ as stated by Walker], SIERRA LEONE: '58–166, S. Leone' (BMNH, abdomen missing) [examined].

Scirpophaga occidentella (Walker) Hampson, 1895: 913; Meyrick, 1933: 376.

Topeutis [*sic*] *occidentella* (Walker) de Joannis, 1927: 189.

♂ (Fig. 162). 16–22 mm. White. Length of labial palpus approximately 1·3 times diameter of compound eye. Fore- and hindwing white, underside fuscous, paler on hindwing.

♀ (Fig. 163). 20–30 mm. White. Fore- and hindwing white on both surfaces; frenulum single-bristled. Anal tuft pale ochreous white.

GENITALIA ♂ (Figs 69, 70). Uncus broad, tapering, constricted abruptly near apex; subteguminal process large, bilobed; anellus with strong spines laterally.

GENITALIA ♀ (Fig. 113). Corpus bursae membranous.

REMARKS. Examination of the holotype of this species has revealed that it is a female and not a male as stated in the original description. As the abdomen is missing it has not been possible to determine other specimens by genitalic characters. Fortunately, however, the female of this species has only a single-bristled frenulum, which at once separates it from the double-bristled frenulum of the other species in this species-group occurring in Africa, and the size in general is also smaller. For these reasons, the specimens examined have been referred to *S. occidentella*.

BIOLOGY. According to the label data of the material examined, the host plant is *Oryza sativa* (Nigeria).

DISTRIBUTION. Senegal, Sierra Leone, Ivory Coast, Nigeria, Zaire, Tanzania, Angola, Mozambique, South Africa, Madagascar, Malawi.

MATERIAL EXAMINED

Senegal: 2 ♂, 3 ♀, Sedhiou, 17–25.vii.1917 (*Castell*) (BMNH); 1 ♂, Thiés, vi.1907 (*Riggenbach*) (BMNH). **Ivory Coast**: 2 ♂, 1 ♀, Bingerville, 5–20.vii.1915 (*Melou*) (BMNH). **Nigeria**: 1 ♀, Badeggi, on *Oryza sativa*, 3.vii.1965 (BMNH); 2 ♂, 2 ♀, Lagos, 17–23.vii.1906 (*Boag*) (BMNH). **Zaire**: 1 ♂, Lubumbashi (Elisabethville), 10.ii.1934 (*Seydel*) (BMNH). **Tanzania**: 2 ♂, Shinyanga, 20.v.1952, 12.v.1954 (*Burtt*) (BMNH). **Angola**: 1 ♂, Mt Moco, Luimbale, 1800–1900 m, 13.iii.1934 (*Jordan*) (BMNH). **Mozambique**: 1 ♀, E. of Mt Chiperone, 2200 ft [660 m], 25.xi.1913 (*Neave*) (BMNH); 1 ♂, Beira, 6.v.1967 (*Jacobs*) (BMNH). **South Africa**: 1 ♂, Port St Johns, Pondoland, x.1923 (*Turner*) (BMNH). **Madagascar**: 8 ♂, Nanisana, xii.1913–i.1932 (*Olsoufieff*) (BMNH); 4 ♂, Parinet, 149 km E. of Tananarivo (*Olsoufieff*) (BMNH); 1 ♂, Mananjary (BMNH); 2 ♂, Diego Suarez, 19.ii.1917 (Melou) (BMNH). **Malawi**: 1 ♂, Zomba, v.1895 (*Rendall*) (BMNH).

Scirpophaga fusciflua Hampson, 1893
(Figs 71, 72, 114, 164, 165, Map 10)

Scirpophaga fusciflua Hampson, 1893: 167, pl. 172, figs 29, 30; Common, 1960: 327. Holotype ♂, SRI LANKA: Pundaloya (*Green*) (BMNH, Pyralidae genitalia slide no. 5022) [examined].

[*Scirpophaga gilviberbis* Zeller; Hampson, 1895: 913. *Scirpophaga fusciflua* Hampson erroneously cited as synonym.]

♂ (Fig. 164). 16–22 mm. Pale ochreous white. Length of labial palpus approximately equal to diameter of compound eye. Forewing white to ochreous white, underside fuscous; hindwing white, underside with costal area suffused with pale fuscous.

♀ (Fig. 165). 21–27 mm. White. Fore- and hindwing white; frenulum single-bristled. Anal tuft greyish white or ochreous yellow.

GENITALIA ♂ (Figs 71, 72). Subteguminal process bilobed; anellus with dense, strong spines laterally.

GENITALIA ♀ (Fig. 114). Ductus bursae and ductus seminalis strongly sclerotized near ostium bursae; corpus bursae membranous, sometimes strongly wrinkled.

REMARKS. *S. fusciflua* appears to be very closely related to the two following species, *S. virginia* and *S. ochroleuca*. The male of *S. fusciflua* can be separated from *S. virginia* by having a bilobed subteguminal process and from *S. ochroleuca* by the relatively short uncus and gnathos and also the uniformly white forewing. No differences could be found in the females of these three species.

BIOLOGY. According to the label data of the material examined the host plant is *Oryza sativa* (Lucknow, India). This species has also been found in rice-fields in Sri Lanka.

DISTRIBUTION. Afghanistan, India, Sri Lanka, Nepal, Thailand, Taiwan.

MATERIAL EXAMINED

Afghanistan: 7 ♂, 7 ♀, Bashgul Valley, Nuristan, 1200 m, 3–21.v.1953 (*Klapperich*) (LN, Karlsruhe); 2 ♂, 2 ♀, 25 km N. of Barikot, Nuristan, 1800 m, 12–17.viii.1963 (*Kasy & Vartian*) (NM, Vienna). **India**: 1 ♀, Lucknow, on *Oryza sativa*, xii.1962 (BMNH); 1 ♂, Tezpur, Assam (BMNH). **Sri Lanka**: 1 ♀, Pundaloya (*Green*) (BMNH) (allotype of *Scirpophaga fusciflua* Hampson); 3 ♂, 1 ♀, Bandarwela, in rice-field, xii.1970 (BMNH); 1 ♂, no further data (BMNH). **Nepal**: 3 ♂, 3 ♀, Jiri, 2000 m, 10–13.viii.1964 (*Dierl*) (ZSBS, Munich); 1 ♂, Katmandu, 1600 m, 30.viii.1964 (*Dierl*) (ZSBS, Munich); 1 ♀, Katmandu, 19.vii.1962 (*Ebert & Falkner*) (ZSBS, Munich); 1 ♂, 2 ♀, Katmandu, 1400 m, 26–29.v.1967 (*Dierl & Schacht*) (ZSBS, Munich); 2 ♂, Katmandu, 4500 ft, 31.vii, 8.viii.1935 (*Bailey*) (BMNH); 1 ♂, Rapti Tal, Megouli, 300 m, 29.iii.–4.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich); 1 ♀, Rapti Tal, Jhawani, 200 m, 15.v.1967 (*Dierl, Forster & Schacht*) (ZSBS, Munich). **Thailand**: 1 ♂, no further data (*Ladell*) (BMNH). **Taiwan**: 3 ♂, 18 ♀, Suishako, 1907 (BMNH).

Scirpophaga ochroleuca Meyrick, 1882

(Figs 73, 74, 115, 166, 167, Map 9)

Scirpophaga ochroleuca Meyrick, 1882: 162; Common, 1960: 326, fig. 7H, pl. 2, fig. 2. Lectotype ♀, [not ♂ as stated by Meyrick], AUSTRALIA: 'Coomooboolaroo, Queensland, GB/77' (BMNH, Pyralidae genitalia slide no. 4020), designated by Common (1960: 327) [examined].

♂ (Fig. 166). 15–18 mm. Pale ochreous. Length of labial palpus approximately 1·2 times diameter of compound eye. Forewing ochreous, underside fuscous; hindwing white with ochreous suffusion on costal half of both surfaces.

♀ (Fig. 167). 19–29 mm. White. Forewing with pale ochreous suffusion, underside white; hindwing white; frenulum single-bristled. Anal tuft pale ochreous white.

GENITALIA ♂ (Figs 73, 74). Gnathos long, slender, subteguminal process slightly bilobed.

GENITALIA ♀ (Fig. 115). As in *S. fusciflua*.

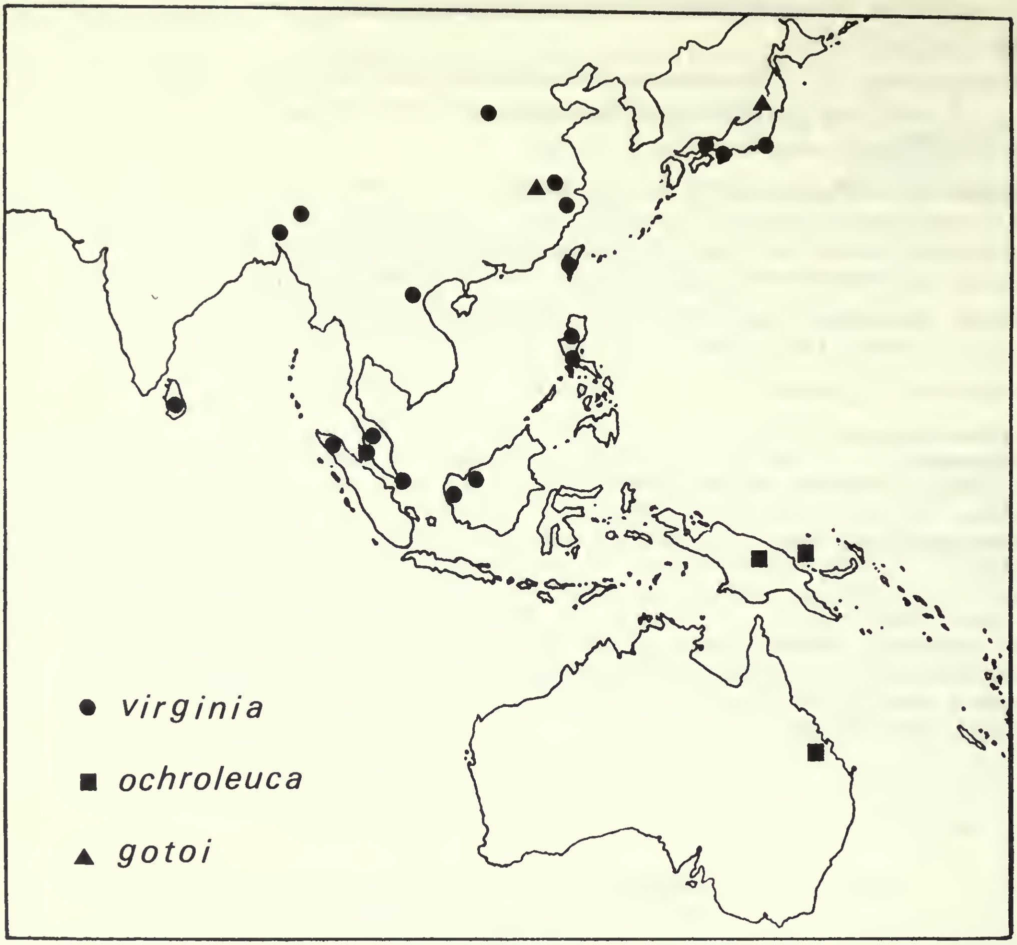
REMARKS. This species is very similar to *S. fusciflua*. The male of *S. ochroleuca* can be distinguished from that species by the ochreous forewings and the long gnathos. In the female, the forewing is always suffused with pale ochreous, and the anal tuft is ochreous white.

BIOLOGY. Unknown.

DISTRIBUTION. Australia, New Guinea.

MATERIAL EXAMINED

Australia: 1 ♀ (not ♂ as stated by Meyrick, 1882 and Common, 1960), same data as lectotype (BMNH, abdomen missing) (paralectotype of *Scirpophaga ochroleuca* Meyrick). **New Guinea**: 1 ♂, 34 ♀, Padwe, Sepik R., 26.x.1957 (*Monroe & Holland*) (CNC, Ottawa); 1 ♂, 1 ♀, Dampier I., 11.iii.1914 (*Meek*) (BMNH).



Map 9

Scirpophaga virginia Schultze, 1908
(Figs 75, 76, 116, 168, 169, Map 9)

Scirpophaga virginia Schultze, 1908: 34. NEOTYPE ♂, PHILIPPINES: Manila, Luzon, 17.i.1913 (*A. E. Wileman*) (BMNH, Pyralidae genitalia slide no. 13465), here designated [examined].

♂ (Fig. 168). 13–17 mm. As in *S. fusciflua* but generally smaller.
♀ (Fig. 169). 16–22 mm. As in *S. fusciflua*. Anal tuft greyish white.

GENITALIA ♂ (Figs 75, 76). As in *S. fusciflua*, but subteguminal process rounded.

GENITALIA ♀ (Fig. 116). As in *S. fusciflua*.

REMARKS. Because of the great similarity between the species in this group, *S. virginia* cannot be recognized with certainty from Schultze's description. It is therefore necessary in the interest of stability of nomenclature to base the identity of *S. virginia* on a neotype.

As mentioned by Schultze (1908: 34), the type-material (holotype ♂ and allotype ♀) was deposited in the Entomological Collection Bureau of Science, Manila, Philippines, where it was destroyed during the Second World War. According to a letter from Miss Clare R. Baltazar, of the same institution, to Dr P. E. S. Whalley (BMNH) ". . .not a single insect specimen in our insect museum was saved during the war; there was a complete destruction of the building. . .".

The species here interpreted as *S. virginia* agrees with Schultze's description. This species is smaller on average than the other species in this group. According to the original description the types were small specimens. The length of the forewing of the holotype was 7·5 mm, which is the same as the length of the forewing in the neotype.

S. virginia was originally collected in Manila in September and October, 1905. The specimen here proposed as the neotype was collected from the same locality in January, 1913.

This species is very close to *S. fusciflua*, the only difference being in the subteguminal process of the male genitalia, which is rounded in this species instead of bilobed as in *S. fusciflua*. No difference was found in the females of these two species.

BIOLOGY. According to the label data of the material examined the host plant is *Oryza sativa* (Dacca, Bangladesh).

DISTRIBUTION. Sri Lanka, Bangladesh, Thailand, West Malaysia, Singapore, Borneo, Sumatra, Philippines, Vietnam, China, Taiwan, Japan.

MATERIAL EXAMINED

Sri Lanka: 3 ♂, no further data (BMNH). **Bangladesh**: 1 ♂, 1 ♀, Dacca, on *Oryza sativa*, 1964 (BMNH); 1 ♂, Chhatak, Sylhet Dist. (*Ewing*) (BMNH). **Thailand**: 2 ♂, 2 ♀, Patalung, at light, 21, 29.iv.1924 (*Evans*) (BMNH). **West Malaysia**: 1 ♂, 1 ♀, Penang, v.1904 (UM, Oxford). **Singapore**: 1 ♂, iii.1905 (*Jones*) (BMNH). **Borneo**: 1 ♂, Pontianak (*Andre*) (BMNH); 2 ♂, 3 ♀, no further data (BMNH). **Sumatra**: 1 ♂, 1 ♀, Tibis, Tinggi, 14.ii–3.iii.1963 (*Diehl*) (BMNH). **Philippines**: 3 ♀, Manila, iii.1913 (*Wileman*) (BMNH); 1 ♂, Los Banos (NMNH, Washington); 1 ♂, 1 ♀, Mt Makiling, Luzon (*Baker*) (NMNH, Washington). **Vietnam**: 1 ♂, Hanoi, 15.x.1923 (*Stevens*) (BMNH). **China**: 5 ♂, 4 ♀, Lungtan, nr Nanking, Kiangsu, 13.vi–27.vii.1933 (*Höne*) (LN, Karlsruhe); 1 ♂, Hoengshan, Hunan, 19.v.1933 (*Höne*) (LN, Karlsruhe); 2 ♂, 2 ♀, Taishan, Shantung, 1550 m, 4.viii–12.ix.1934 (*Höne*) (LN, Karlsruhe). **Taiwan**: 2 ♂, 2 ♀, Takow, 7.viii–4.ix.1904 (*Wileman*) (BMNH). **Japan**: 1 ♂, Ikada, Osaka, 5.vii.1951 (*Mutuura*) (CNC, Ottawa); 4 ♂, 2 ♀, Sakai, Osaka, 12.vii–3.viii.1948, 9.vii–28.viii.1949 (*Mutuura*) (CNC, Ottawa); 1 ♂, Hieisan, Kyoto, 24.vii.1948 (*Mutuura*) (CNC, Ottawa); 1 ♂, 2 ♀, Sakaisi, Honshu, 26.vi.1954 (*Mutuura*) (CNC, Ottawa); 1 ♂, Miyamamuka, 29.vii.1948 (*Mutuura*) (CNC, Ottawa); 2 ♂, 5 ♀, Yokohama (*Höne*) (LN, Karlsruhe); 1 ♂, Yokohama, ix.1911 (BMNH).

Scirpophaga subumbrosa Meyrick, 1933
(Figs 77, 78, 117, 170, 171, Map 12)

Scirpophaga subumbrosa Meyrick, 1933: 376. Holotype ♂, ZAIRE: Kitobola, 1911 (*Rovere*) (MRAC, Tervuren) [examined].

♂ (Fig. 170). 22–28 mm. Pale ochreous white. Length of labial palpus approximately 2 times diameter of compound eye. Forewing with colour varying from pale ochreous white to pale ochreous, underside fuscous; hindwing pale ochreous white on both surfaces, costal area suffused with ochreous, stronger on underside.

♀ (Fig. 171). 28–40 mm. White. Fore- and hindwing white on both surfaces; frenulum double-bristled. Anal tuft pale ochreous yellow.

GENITALIA ♂ (Figs 77, 78). Valva relatively narrow, costal and ventral margin more or less parallel; anellus with dense, strong spines.

GENITALIA ♀ (Fig. 117). Ductus bursae lined with spines on one side; corpus bursae with dense spines.

REMARKS. The whitish forewings of the male of *S. subumbrosa* distinguish it from *S. marginepunctella,* which has ochreous forewings with markings. The genitalia of these two species are very similar in having the anellus covered with strong spines, but the valva of *S. subumbrosa* is narrower distally. In the female genitalia, this species differs from others in the *occidentella*-group in having the corpus bursae densely lined with spines.

BIOLOGY. According to the label data of the material examined the host-plant is *Oryza sativa* (Nigeria, Sierra Leone).

DISTRIBUTION. Senegal, Sierra Leone, Ghana, Nigeria, Sudan, Ethiopia, Zaire, Tanzania, Zambia, Malawi, Mozambique, Madagascar.

Material examined

Senegal: 4 ♂, 1 ♀, Sedhiou, 3–8.vii.1917 (*Castell*) (BMNH). **Sierra Leone**: 1 ♀, Mange, on *Oryza sativa,* 24.ix.1964 (*Jordan*) (BMNH). **Ghana**: 1 ♂, 1 ♀, Bolgatanga, iv.1962 (*Lewis*) (BMNH); 1 ♀, Kete Krachi (*Cardinall*) (BMNH); 1 ♂, 1 ♀, Navaro, vii.1923 (*Cardinall*) (BMNH). **Nigeria**: 3 ♂, Abinsi, 5.v.1912 (BMNH); 7 ♂, 8 ♀, Badeggi, on *Oryza sativa,* 23.vii–3.viii.1965 (BMNH); 4 ♀, Badeggi, on *Oryza sativa* (BMNH); 1 ♂, 2 ♀, Lokoja, x.1904 (*Cator*) (BMNH); 1 ♂, 1 ♀, Warri, vi.1897 (*Roth*) (BMNH); 1 ♂, 2 ♀, Zungeru, 28.x.1910–15.v.1911 (*Macfie*) (BMNH); 1 ♂, 1 ♀, Agberi, 26.vii.–9.viii.1901 (*Ansorge*) (BMNH). **Sudan**: 2 ♂, White Nile, 511–520 m, S. of Khartoum, 12.x.1918 (*Wilson*) (UM, Oxford). **Ethiopia**:1 ♂, Ogotok, 13.v.1904 (*Zaphiro*) (BMNH). **Zaire**: 1 ♂, Kitobola, 1911 (*Rovere*) (BMNH) (paratype of *Scirpophaga subumbrosa* Meyrick); 2 ♂, 1 ♀, Katanga, xi.1926–ii.1927 (BMNH); 2 ♂, Lulua, 10.iv.1932 (BMNH). **Tanzania**: 1 ♂, 1 ♀, Mbamba Bay, 12–16.iv.1936 (*Zerny*) (NM, Vienna). **Zambia**: 1 ♀, Luangwa, 1800–2000 ft [540–600 m], 5.iii.1908 (UM, Oxford). **Malawi**: 1 ♀, Mlanje, 6500 ft [1970 m], 5.x.1913 (*Neave*) (BMNH); 3 ♂, 1 ♀, SW. of Lake Chilwa, 11.i.1914 (*Neave*) (BMNH). **Mozambique**: 1 ♂, E. of Mt Chiperone, 2200 ft [660 m], 26.xi.1913 (*Neave*) (BMNH); 1 ♂, Chinde, 4.viii.1899 (*Jersey*) (BMNH). **Madagascar**: 6 ♂, 2 ♀, Sambirano (MNHN, Paris); 4 ♂, no further data (MNHN, Paris).

Scirpophaga marginepunctella (de Joannis, 1927) **comb. n.**

(Figs 79, 80, 118, 172, 173, Map 13)

Schoenobius marginepunctellus de Joannis, 1927: 189, pl. 8, fig. 6. Holotype ♂, MOZAMBIQUE: Makulane, x.–xii.1907, Coll. Dr. G. Audéoud (MHN, Geneva) [examined].

♂ (Fig. 172). 25–30 mm. Ochreous. Length of labial palpus approximately 2·6 times diameter of compound eye. Forewing ochreous, markings as in male of *S. nivella,* underside fuscous; hindwing white, costal area suffused with pale fuscous on both surfaces.

♂ (Fig. 173). 36–44 mm. White. Forewing usually suffused with very pale ochreous white on upperside, hindwing white; frenulum double-bristled. Anal tuft ochreous yellow.

Genitalia ♂ (Figs 79, 80). Valva broad distally; anellus with dense spines.

Genitalia ♀ (Fig. 118). Corpus bursae membranous, sparsely lined with minute spines in basal half.

Remarks. The male of this species is similar to the male of *S. nivella* externally, but the labial palpus of *S. marginepunctella* is much longer. *S. marginepunctella* is found only in Africa while *S. nivella* is Australasian. The genitalia are similar to those of *S. subumbrosa,* the diagnostic difference being the width of the valva which is broader distally in *S. marginepunctella.* Externally these two species are quite distinct. *S. marginepunctella* has ochreous forewings with markings while *S. subumbrosa* has plain whitish forewings.

The female of *S. marginepunctella* can be distinguished from the other white Afrcian species by the ochreous yellow anal tuft and the double-bristled frenulum. The genitalia have a membranous corpus bursae with very few spines, similar to that of *S. serena,* but the ostium bursae lacks the longitudinal wrinkling towards the ductus bursae found in *S. serena.*

Biology. Unknown.

Distribution. Senegal, Nigeria, Sudan, Zaire, Angola, Botswana, Mozambique, Madagascar.

Material examined

Senegal: 1 ♀, Sedhiou, 5–12.vii.1917 (*Castell*) (BMNH). **Nigeria**: 1 ♀, Lokoja, x.1904 (*Cator*) (BMNH). **Sudan**: 1 ♂, 1 ♀, White Nile, 511–520 m S. of Khartoum, 12.x.1918 (*Wilson*) (UM, Oxford); 1 ♂, 2 ♀, White Nile, Khor et 'Atash, 7.ii.1912 (*Longstaff*) (BMNH); 3 ♀, Mongalla, 20.x.1917 (*Yardley*) (BMNH); 1 ♀, Wau, 6.ii.1912 (*Longstaff*) (BMNH). **Zaire:** 1 ♀, Ankoro, 6.iii.1926 (BMNH); 1 ♀, Lualaba R. nr Mayumba, 14.viii.1931 (*Cockerell* (BMNH); 1 ♂, Lulua, 10.iv.1932 (BMNH); 1 ♀, Katanga, x.1930 (BMNH); 1 ♀, no further data (BMNH). **Angola**: 1 ♀, Boma, x.1903 (*Christy*) (BMNH). **Botswana**: 3 ♂, Chobe, at black light, 20.ii.1970 (*Ingram*) (BMNH). **Mozambique**: 1 ♂, same data as holotype (MHN, Geneva) [this specimen was misidentified as ♀ and erroneously designated as 'allotype' by de Joannis]; 1 ♂, Beira, 12.v.1907 (MNHN, Paris) [abdomen missing] (both paratypes of *Scirpophaga marginepunctella* de Joannis); 1 ♀, Makulane, x.–xi.1907 (MNHN, Paris). **Madagascar**: 2 ♂, Sambirano (MNHN, Paris) (paratypes) [one specimen was misidentified as ♀ by de Joannis]; 1 ♀, Manangara, xi.1918 (*Le Moult*) (BMNH); 1 ♂, Maroantsetra, iv.1952 (MNHN, Paris); 1 ♂, 1 ♀, Sambirano (MNHN, Paris); 1 ♀, Sambirano, 16, 17.xii.1963 (*Viette & Soga*) (MNHN, Paris); 1 ♂, no further data (MNHN, Paris).

Scirpophaga serena (Meyrick, 1935) **comb. n.**
(Figs 81, 82, 119, 174, 175, Map 14)

Schoenobius serenus Meyrick, 1935: 554. Holotype ♀, ZAIRE: Lulua, Kafakumba, iv.1932 (*F. G. Overlaet*) (MRAC, Tervuren) [examined].

♂ (Fig. 174). 30–35 mm. Dark ochreous. Length of labial palpus approximately 3 times diameter of compound eye. Forewing dark ochreous, markings as in *S. marginepunctella*; hindwing suffused with fuscous on distal half.

♀ (Fig. 175). 46–53 mm. Head and palpi pale ochreous white. Forewing with costal margin pale ochreous white, the rest varying from pale ochreous to ochreous, underside suffused with pale fuscous; hindwing white; frenulum double-bristled. Anal tuft ochreous yellow.

GENITALIA ♂ (Figs 81, 82). Subteguminal process large, lobe-like; anellus with dense, strong spines laterally; valva relatively long and narrow.

GENITALIA ♀ (Fig. 119). Ostium bursae broad, membranous, with longitudinal wrinkles towards ductus bursae; corpus bursae membranous.

REMARKS. In Africa, the male of *S. serena* can be confused only with *S. marginepunctella* externally, but the colour of *S. serena* in general is darker and the size is larger. With regard to the genitalia, the shape of the subteguminal process, the long valva and the dense spines on both sides of the anellus are characteristic of *S. serena*. The female genitalia are very similar to those of *S. marginepunctella*, but the longitudinal wrinkles in the ostium bursae towards the ductus bursae, which are absent in *S. marginepunctella*, are characteristic of *S. serena*.

BIOLOGY. Unknown.

DISTRIBUTION. Zaire, Angola.

MATERIAL EXAMINED

Zaire: 1 ♂, Lubumbashi (Elisabethville), 25.xi.1936 (*Seydel*) (MRAC, Tervuren); 1 ♂, Kafakumba, ix.1932 (*Overlaet*) (MRAC, Tervuren); 1 ♀, Kafakumba, xii.1927 (BMNH); 1 ♂, Katanga, xii.1928 (*Seydel*) (MRAC, Tervuren); 1 ♀, Kapanga, vii.1933 (*Overlaet*) (MRAC, Tervuren); 2 ♂, Sandoa, 24.i.1919, ii.1931 (*Overlaet*) (MRAC, Tervuren); 2 ♂, Sandoa, 30.x., 14.xi.1920 (BMNH); 2 ♂, Lulua, xi.1930, i.1931 (*Overlaet*) (BMNH). **Angola**: 2 ♀, Upper Cubango-Cunene, 550 ft [160 m], xi.1928 (*Barns*) (BMNH).

Scirpophaga goliath Marion & Viette, 1953
(Figs 120, 176, Map 14)

Scirpophaga goliath Marion & Viette, 1953: 39, fig. 1. Holotype ♀, MADAGASCAR: Tananarive, Parc de Tsimbazaza, 1200 m, 14.i.1952 (*Viette*) (MNHN, Paris) [not examined].

♂. Unknown.

♀ (Fig. 176). 46–52 mm. Head and palpi ochreous white. Forewing fuscous, costal area pale ochreous white, underside fuscous; hindwing white; frenulum double-bristled. Anal tuft ochreous yellow.

GENITALIA ♀ (Fig. 120). As in *S. serena*.

REMARKS. The female genitalia of this species are similar to those of *S. serena*, and the length of the wing expanse is also about the same. The only difference observed is in the forewing, which is narrower and fuscous in *S. goliath* but ochreous and slightly broader in *S. serena*. The pale ochreous white suffusion on the costal area extends from the base of the wing to the apex of R_2 in *S. serena*, and to R_3 in *S. goliath*. When the male is known, it is possible that *S. goliath* may prove to be conspecific with *S. serena*, since in this group colour is often variable. On the other hand it may be a good species because in the *occidentella*-group it has been found that the female genitalia of two species may be similar. At present *S. goliath* is considered to be distinct from *S. serena*.

BIOLOGY. Unknown.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED

Madagascar: 1 ♀, Plateaux de l'Imerina, Tananarive, Parc de Tsimbazaza, 1200 m, 19.i.1952 (*P. Viette*) (BMNH, Pyralidae genitalia slide no. 12907) (paratype of *Scirpophaga goliath* Marion & Viette); 1 ♀, Belroka, 17.ii.1955 (*Diehl*) (BMNH).

The *lineata*-group

Labial palpus long with spreading scales. Forewing with vein R_1 anastomosed with *Sc*. Frenulum in both sexes single-bristled.

GENITALIA ♂. Uncus and gnathos relatively short, strongly curved towards each other at apices; tegumen with dorsal sclerotized thickening somewhat triangular; subteguminal process strongly sclerotized, plate-like, originating very close to appendices angulares; valva not strongly sclerotized; manica with uniformly arranged minute spines; aedeagus slender, more or less uniform in diameter, vesica with minute spines.

GENITALIA ♀. Ostium bursae relatively broad, membranous; ductus bursae membranous, section between ostium bursae and ductus seminalis constricted, lined with sclerotized plate, U-shaped in cross section; ductus seminalis arising from ductus bursae closer to ostium bursae than corpus bursae; corpus bursae with dense spines; papillae anales wrinkled and leathery near tip.

The *lineata*-group consists of three species, *S. lineata, S. aurivena* and *S. auristrigella*. The group has the plate-like subteguminal process in the male genitalia similar to those of the *praelata*-group but the position of origin is different. In the *lineata*-group, the subteguminal process originates at a point very near to the appendices angulares where the valva attaches to the tegumen, while in the *praelata*-group, the base of the subteguminal process is broad and the valva is more sclerotized than that in the *lineata*-group. The aedeagus is also different; in the *praelata*-group cornuti are present, while in the *lineata*-group they are absent.

In the females the apex of the papillae anales is wrinkled and leathery near the tip, which is a characteristic of this species-group.

Key to species of the *lineata*-group

Males

1 Forewing white, with markings forming a pattern (Fig. 177) . . . . . . **lineata** (p. 240)
– Forewing pale yellow, without markings, sometimes with one dark fuscous spot . . . 2
2 Forewing without spot; subteguminal process with pointed apex, or truncate (Fig. 85) **aurivena** (p. 242)
– Forewing with one dark fuscous spot; subteguminal process with posterior margin produced to form a spine (Fig. 87). . . . . **auristrigella** (p. 242)

Females

Only the female of *S. lineata* is known.

Scirpophaga lineata (Butler, 1879) comb. n.

(Figs 83, 84, 123, 177, 178, Map 10)

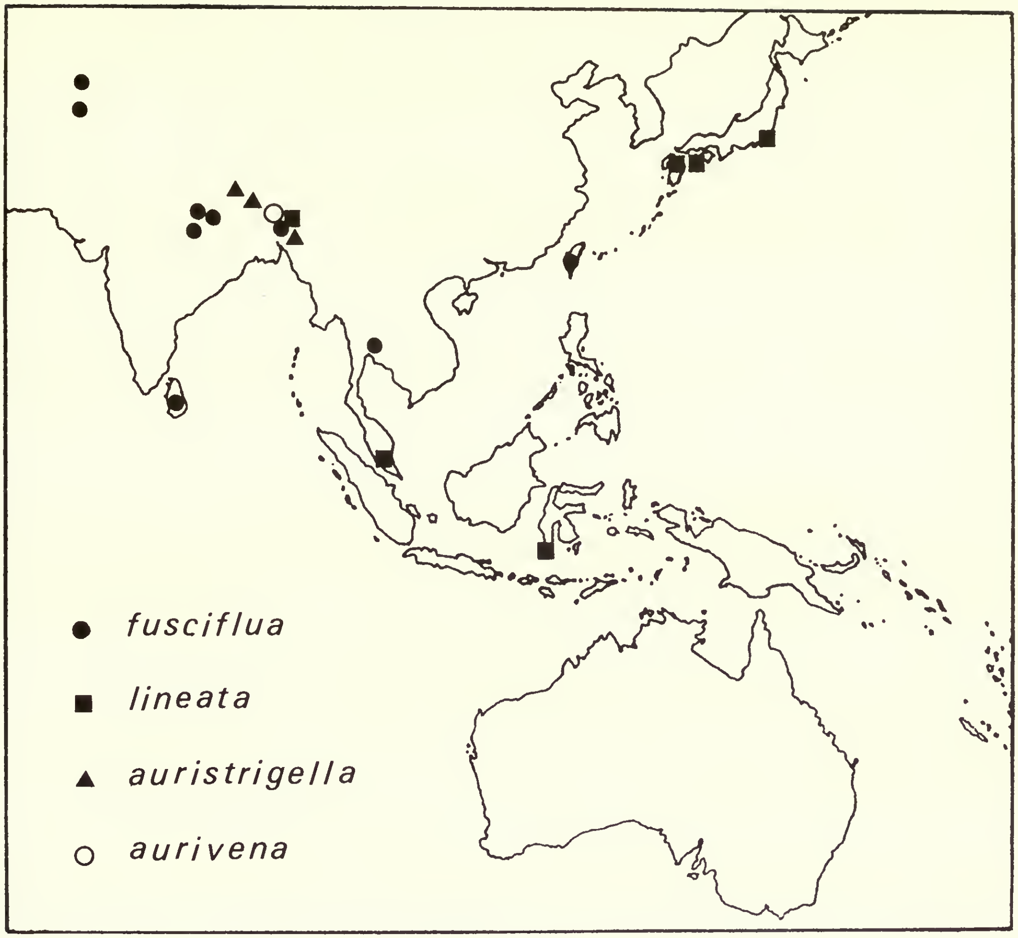
Apurima lineata Butler, 1879: 457. Holotype ♀, JAPAN: [Yokohama] (BMNH, Pyralidae genitalia slide no. 6329) [examined].

Schoenobius lineatus (Butler) Hampson, 1895: 917; Leech, 1901: 402; Marumo, 1934: 2, 21, pl. 1, fig. 7, pl. 2, fig. 6, pl. 3, fig. 6.

♂ (Fig. 177). 18–23 mm. White. Labial palpus with expanding scales, in length approximately 3–4 times diameter of compound eye. Forewing white, interspaces of veins suffused with light brown, an oblique light brown band from apex to middle of ventral margin, a dark fuscous spot at lower angle of cell, underside fuscous; hindwing white.

♀ (Fig. 178). 22–26 mm. Coloration and markings as in male. Frenulum single-bristled. Anal tuft white.

GENITALIA ♂ (Figs 83, 84). Subteguminal process strongly sclerotized, truncate and plate-like; valva narrow apically; aedeagus slender, vesica with minute spines.



Map 10

Genitalia ♀ (Fig. 123). Ostium bursae relatively broad, membranous; ductus bursae membranous, section near ostium bursae constricted, lined with sclerotized plates; ductus seminalis arising from ductus bursae closer to ostium bursae than to corpus bursae; corpus bursae with dense spines; papillae anales wrinkled and slightly sclerotized near tip.

Remarks. The male genitalia of this species are very similar to those of *S. aurivena* and *S. auristrigella,* especially the former with regard to the shape of the subteguminal process. The female genitalia are also similar to those of the other two species. In both sexes of *S. lineata,* the white forewing with markings connot be confused with the plain forewings (sometimes with a spot) of *S. aurivena* and *S. auristrigella.*

Biology. The host-plant is *Oryza sativa* in Japan (Marumo, 1934: 2, 3).

Distribution. Japan, India, West Malaysia, Sulawesi.

Material examined

Japan: 1 ♂, 3 ♀, Yokohama, 22-24.vii.1898 (*Wileman*) (BMNH); 2 ♂, Yokohama, 14.vi., vii.1910 (*Höne*) (LN, Karlsruhe); 1 ♂, Yoshino, 10.vii.1899 (*Wileman*) (BMNH); 2 ♀, Yoshino, vii.1900 (*Wileman*) (BMNH); 1 ♂, 1 ♀, Hikosan, 5,7.viii.1954 (*Kuroko*) (CNC, Ottawa); 1 ♀, Inunakisan, Osaka, 3.ix.1956 (*Mutuura*) (CNC, Ottawa). **India**: 2 ♀, Khasis, Shillong, 5000 ft [1500 m], 29.vi., 1.vii.1928 (*Fletcher*) (BMNH). **West Malaysia**: 1 ♀, Selangor, Buki Kutu, 3500 ft [1050 m], at light, 14.iv.1926 (*Pendlebury*) (BMNH). **Sulawesi**: 1 ♀, Tjamba nr Maros, 1500 ft [450 m], ii.1938 (*Kalis*) (BMNH).

Scirpophaga aurivena (Hampson, 1903) **comb. n.**

(Figs 85, 86, 179, Map 10)

Schoenobius aurivena Hampson, 1903: 20. Holotype ♂, INDIA: Khasis [Khasi Hills], (BMNH, Pyralidae genitalia slide no. 13475) [examined].

♂ (Fig. 179). 19–22 mm. Pale yellow. Labial palpus suffused with yellow externally, in length approximately 3 times diameter of compound eye. Forewing pale yellow, interspaces of veins yellow, underside fuscous; hindwing white.

♀. Unknown.

GENITALIA ♂ (Figs 85, 86). Very similar to those of *S. lineata*. In the holotype, the subteguminal process has a pointed apex and is quite distinct from that of *S. lineata*, but variation occurs in the other specimens, the subteguminal process in them being somewhat truncate as in *S. lineata*.

REMARKS. This species is very similar to *S. auristrigella* externally, but in *S. aurivena* the forewing is without the spot which is usually present in *S. auristrigella*.

Three females from Khasi Hills are similar externally to the males of *S. aurivena* and *S. auristrigella*; however, at present it is not possible to match the sexes and breeding experiments are needed to associate them. The genitalia of these three females are very similar to those of *S. lineata*.

BIOLOGY. Unknown.

DISTRIBUTION. India.

MATERIAL EXAMINED

India: 3 ♂, Khasi Hills, vi.,x.1894 (BMNH).

Scirpophaga auristrigella (Hampson, 1895) **comb. n.**

(Figs 87, 88, 180, Map 10)

Schoenobius auristrigellus Hampson, 1895: 916; 1896: 49. Holotype ♂, BHUTAN: 28.vi.1895 (*Dudgeon*) (BMNH, Pyralidae genitalia slide no. 13474) [examined].

♂ (Fig. 180). 20–26 mm. Similar to *S. aurivena* but forewing usually with a dark fuscous spot at lower angle of cell. In the holotype, forewing with oblique yellow line from the apex to the middle of the ventral margin. This line is absent in some specimens and in others it is present along subterminal margin.

♀. Unknown.

GENITALIA ♂ (Figs 87, 88). Similar to *S. lineata* and *S. aurivena* but subteguminal process with posterior margin produced to form a spine.

REMARKS. Very similar to *S. aurivena* but the forewing usually has a dark fuscous spot. In the male genitalia, the posterior margin of the subteguminal process, produced to form a spine, is characteristic of this species.

BIOLOGY. Unknown.

DISTRIBUTION. India, Bhutan.

MATERIAL EXAMINED

India: 15 ♂, Khasi Hills, v.–viii.1894 (BMNH); 2 ♂, Khasi Hills (UM, Oxford); 1 ♂, Cherra[pungji], Assam (BMNH); 1 ♂, Sikkim, 17.vii.1889 (*Pilcher*) (BMNH).

The *incertulas*-group

Forewing with vein R_1 curved towards *Sc*, sometimes coincident with it. Frenulum in male a single bristle, in female with single or double bristles.

GENITALIA ♂. Uncus and gnathos moderately long and slender; tegumen with sclerotized thickening somewhat triangular; subteguminal process spine-like; aedeagus slender, vesica with minute spines, two adjacent unequal curved spined, cornuti present.

GENITALIA ♀. Ostium bursae broad, membranous, wrinkled with small spines; ductus bursae membranous; ductus seminalis arising near ostium bursae; corpus bursae lined with spines in basal three-quarters.

The *incertulas*-group consists of two economically important species, *S. incertulas* and *S. innotata*. Both of them are very serious pests of rice in Asia and were considered by Common (1960) to be in a separate genus, *Tryporyza*, which in this study is considered to be a synonym of *Scirpophaga* (see p. 196).

Key to species of the *incertulas*-group

Males

1 Forewing ochreous, with markings; subteguminal process a bifid spine (Fig. 89) **incertulas** (p. 243)
– Forewing white or pale ochreous white, without markings; subteguminal process a single curved spine (Fig. 91). . . . . **innotata** (p. 246)

Females

1 Forewing pale yellow with one dark fuscous spot at lower angle of cell; ostium bursae strongly wrinkled, lined with minute spines; corpus bursae with dense spines in basal three-quarters (Fig. 121) . . . . **incertulas** (p. 243)
– Forewing white without spot; genitalia as above (Fig. 122) . . . . . . **innotata** (p. 246)

Scirpophaga incertulas (Walker, 1863) **comb. n.**
(Figs 89, 90, 121, 181, 182, Map 11)

Chilo incertulas Walker, 1863*a*: 143. Holotype ♂, BORNEO: Sarawak, Saunders' Coll. (BMNH, Pyralidae genitalia slide no. 2463) [examined].

Catagela ?admotella Walker, 1863*a*: 192. Holotype ♂, SRI LANKA: [Colombo, x.1857 (*Nietner*)] (BMNH, Pyralidae genitalia slide no. 2465) [examined]. [Synonymized with *incertulas* Walker by Hampson, 1895: 916.]

Schoenobius punctellus Zeller, 1863: 4. LECTOTYPE ♀, JAVA: 'Java Tengstr.' (BMNH, Pyralidae genitalia slide no. 6346), here designated [examined]. [Synonymized with *incertulas* Walker by Shiraki, 1917: 2.]

Schoenobius minutellus Zeller, 1863: 5. LECTOTYPE ♂, JAVA: 'Java, Tengstr.' (BMNH, Pyralidae genitalia slide no. 11067) here designated [examined]. [Synonymized with *incertulas* Walker by Hampson, 1895: 916.]

Tipanaea bipunctifera Walker, 1863*b*: 523. Holotype ♀ [not ♂ as stated by Walker], BORNEO: Saunders' Coll. (BMNH, Pyralidae genitalia slide no. 6296) [examined]. [Synonymized with *incertulas* Walker by Shiraki, 1917: 2.]

Chilo gratiosellus Walker, 1864: 967. LECTOTYPE ♀, SRI LANKA: 'Ceylon' [Colombo, x.1857 (*Nietner*)] (BMNH, Pyralidae genitalia slide no. 13473), here designated [examined]. [Synonymized with *incertulas* Walker by Shiraki, 1917: 2.]

[*Chilo*] *incertellus* Walker; Walker, 1864: 1069.

Apurima gratiosella (Walker) Butler, 1880: 690.

Schoenobius bipunctifera (Walker) Moore, 1886: 385, pl. 184, fig. 13; Leech, 1901: 403.

Catagela admotella Walker; Moore, 1886: 386.

Schoenobius bipunctiferus (Walker); Hampson, 1895: 915.

Schoenobius incertulas (Walker) Hampson, 1895: 916; 1896: 48; Jepson, 1954: 9, pl. 1; Martin, 1958: 187, figs 3, 7, pl. 6, figs 2, 3.

Schoenobius bipunctifer (Walker); Hampson, 1896: 48; Strand, 1918: 262.

Schoenobius incertellus (Walker); Shiraki, 1917: 1–256, pls 1–22; Fletcher, 1932: 276; Shibuya, 1928: 63, pl. 4, figs 18, 25; de Joannis, 1929: 609; Marumo, 1934: 18, pl. 1, figs 8, 9, pl. 2, figs 1–3, 5, pl. 3, fig. 10, pl. 4, fig. 5, pl. 5, figs 1–5.

Schoenobius bipunctifer ab. *quadripunctellifera* Strand, 1918: 263.

Tryporyza incertulas (Walker) Common, 1960: 341; Kapur, 1967: 6, 23.

♂ (Fig. 181). 20–24 mm. Ochreous. Length of labial palpus approximately 3 times diameter of compound eye. Forewing ochreous, markings as in *S. nivella*, underside fuscous; hindwing white with ochreous suffusion in costal half.

♀ (Fig. 182). 23–33 mm. Pale yellow. Labial palpus pale yellowish ochreous. Forewing yellowish ochreous with one dark fuscous spot at the lower angle of the cell; hindwing white with yellowish ochreous suffusion in costal half; frenulum double-bristled. Anal tuft pale ochreous white.

Genitalia ♂ (Figs 89, 90). Uncus and gnathos long, slender; tegumen with dorsal sclerotized thickening somewhat triangular in shape; subteguminal process a bifid spine; aedeagus slender, vesica with small spines, two adjacent unequal curved spined cornuti present.

Genitalia ♀ (Fig. 121). Ostium bursae membranous, strongly wrinkled; lined with minute spines; corpus bursae with spines in the basal three-quarters.

Remarks. The name '*incertellus*' was mentioned first in the index to Walker's catalogue (vol. 30, 1864: 1069) referring to the page of the description for *incertulas* (vol. 27, 1863: 143). Fletcher (1923: 276), without giving any evidence, stated that *incertulas* was an error in manuscript or printing but corrected to *incertellus* in the index. Since *incertulas* has priority and there is no evidence of original misspelling, this name is used here.

The male of this species is similar externally to the male of *S. nivella,* especially in the forewing markings, but it can be distinguished by the longer labial palpus (about 3·0 times diameter of compound eye in *S. incertulas* and 1·3 times in *S. nivella*), and the forewing in *S. incertulas* is dull, not shining as in *S. nivella*.

The male genitalia of *S. incertulas* are very similar to those of *S. innotata,* but the subteguminal process of *S. incertulas* is a bifid spine while in *S. innotata* it is a single spine. No differences could be found in the female genitalia of these two species. Externally *S. incertulas* is quite different from *S. innotata* in both sexes.

Biology. According to the label data of the material examined, and published data, the host plant is *Oryza sativa.*

Shiraki (1917), when studying *S. incertulas* in Taiwan, tried to find the alternative host plants of this species. By checking the stems of 15 different plants in the field every month from 1909–1911, he could not find a single larva of *S. incertulas* feeding on them. The plants were *Miscanthus sinensis, Zizania latifolia, Panicum proliferum, Imperata arundinacea* var., *Erianthus* sp., *Eragrostis major, Ischaemum rugosum* var., *Paspalum scrobiculatum, Calamagrostis epigejos* var., *Scirpus mucronatus, Scirpus lacustris, Panicum repens,* sugar-cane, barley and teosinte.

Fletcher & Ghosh (1920) were of the opinion that the true *S. incertulas* had not been observed feeding on any plant other than rice. They criticized a report by Kasargode and Despande that *S. incertulas* is also found on *Coix lachryma, Ischoemum aristatum, Andropogon odoratus* and *Anthistiria ciliata* in India.

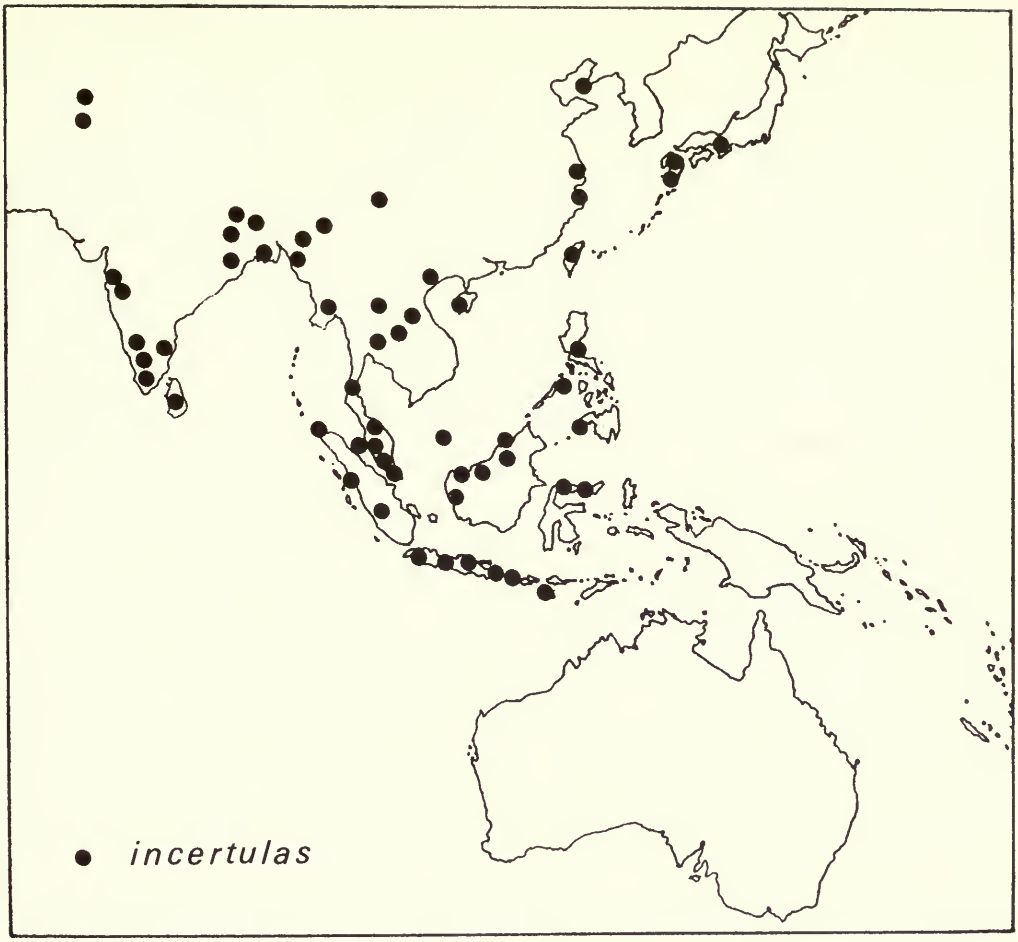
Box (1953) listed *Schoenobius bipunctifer* (a synonym of *S. incertulas*) as a pest of sugar-cane in India, Burma, Malaya, China and the Philippines. The occurrence of *S. incertulas* on sugar-cane is also supported by a label on a female specimen from an unknown locality, although it is possible that this specimen has the wrong label attached to it. Whether sugar-cane is an alternative host plant for *S. incertulas* remains unconfirmed and needs to be investigated by field work. Logothetis (1950) mentioned volunteer rice and many gramineous plants, especially wild *Cyperus,* as the host plants of *S. incertulas.*

The life history of *S. incertulas* has been studied by many authors. The fullest details were given by Shiraki (1917), who wrote a monograph concerning nearly all aspects of this species. Fletcher & Ghosh (1920) investigated the species in India, Kiritani & Iwao (1967) studied it in a temperate region, and Banerjee & Pramanik (1967) in the tropics. The life history of *S. incertulas* is also mentioned by Logothetis (1950) and Grist & Lever (1969).

Distribution. Afghanistan, Nepal, India, Sri Lanka, Bangladesh, Burma, Vietnam, Thailand, West Malaysia, Singapore, Sumatra, Java, Borneo, Sumba, Sulawesi, Philippines, Taiwan, Hong Kong, China, Japan.

Material examined

Afghanistan: 1 ♂, 2 ♀, Sarobi, 1100 m, 10.v.–13.ix.1961 (*Ebert*) (ZSBS, Munich); 3 ♂, 2 ♀, Sarobi, 1100 m, 17.iv.–27.ix.1961 (*Ebert*) (LN, Karlsruhe). **Nepal**: 6 ♂, 3 ♀, Rapti Tal, Megouli, 300 m, 29.iii.–4.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich); 1 ♂, Rapti Tal, Jhawani, 200 m, 16.v.1967 (*Dierl, Forster & Schacht*) (ZSBS, Munich); 1 ♂, Bhimpedi, 400 m, 4–7.iv.1962 (*Ebert & Falkner*) (ZSBS, Munich); 2 ♀, Thangpoche, 3980 m, 9.viii.1964 (*Löffler*) (ZSBS, Munich); 3 ♀, Katmandu, 1400 m, 27–29.v.1967 (*Dierl & Schacht*) (ZSBS, Munich); 1 ♀, Monahari, Khola, Belwa, 350 m, 10.v.1967 (*Dierl, Forster & Schacht*) (ZSBS, Munich). **India**: 2 ♂, Calcutta (BMNH) (paralectotypes of *Schoenobius minutellus* Zeller); 1 ♀, Assam, at



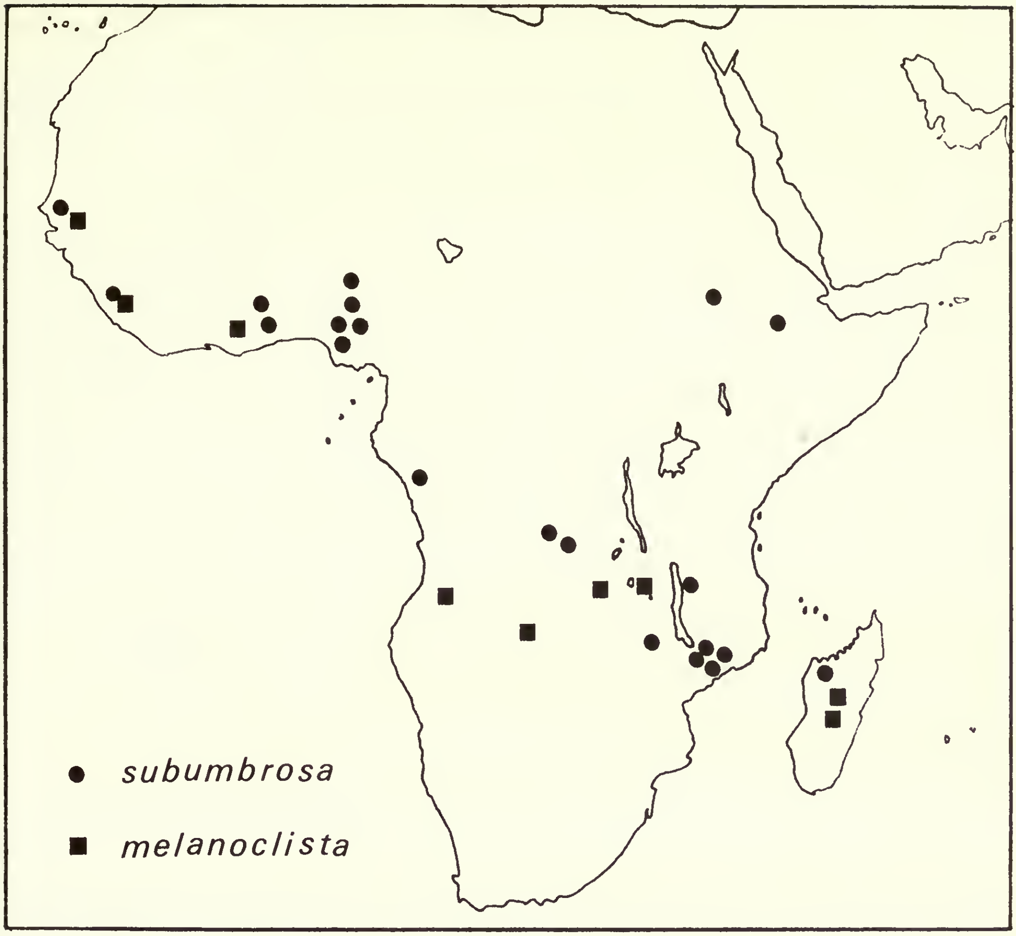
Map 11

rest on *Scirpus* sp., iii.1965 (BMNH); 2 ♂, Pusa, 30.iii.1927 (*Hassan*) (BMNH); 2 ♀, Pusa, at light, 9.viii.1926 (*Pillai*) (BMNH); 1 ♀, Pusa, 6.iii.1929 (*Fletcher*) (BMNH); 4 ♀, Malabar, Cochin, 23–27.xii.1941 (*Graham*) (BMNH); 4 ♀, Nilgiris Hills (BMNH); 7 ♀, Trichinopoly (*Castets*) (BMNH); 8 ♂, 15 ♀, Mahe (BMNH); 3 ♂, 5 ♀, Madras, xii.1896–iii.1897 (BMNH); 3 ♂, 10 ♀, Calcutta (BMNH); 1 ♂, 1 ♀, Bombay, viii.1890 (BMNH); 1 ♀, Bombay, x.1883 (BMNH); 1 ♀, Bombay (BMNH); 1 ♂, 1 ♀, Poona, xi.1882 (BMNH); 2 ♀, Tezpur, Assam (BMNH); 1 ♀, Assam (BMNH); 1 ♀, Uttamapalaiyam, 5000 ft [1500 m], xii.1932 (*Cantley*) (BMNH); 1 ♂, Palni (BMNH); 1 ♀, Belgaum, vii.1896 (BMNH); 1 ♀, Ganjam (BMNH). **Sri Lanka**: 2 ♀, Ceylon [Colombo, x.1857 (*Nietner*)] (BMNH) (paralectotypes of *Chilo gratiosellus* Walker); 4 ♀, Colombo, i.1896, vii.1901, viii.1908 (BMNH); 4 ♀, Colombo, 7.ii., 22.v., 16–17.vii.1945 (*Howord*) (BMNH); 1 ♀, Colombo, 24.xii.1907 (*Meade Waldo*) (BMNH); 1 ♀, Colombo (BMNH); 1 ♂, 8 ♀, Kandy, iv.1894, i.1902, iii.1904, ix.–xii.1907 (BMNH); 1 ♂, 1 ♀, Maskeliya (BMNH); 3 ♂, 3 ♀, Puttalam (BMNH); 2 ♂, Hambantola (BMNH); 1 ♀, Gampola, xii.1905 (BMNH); 2 ♂, 5 ♀, no further data (BMNH). **Bangladesh**: 1 ♀, Chittagong (BMNH); 1 ♀, Bengal, v.1894 (BMNH). **Burma**: 2 ♂, 1 ♀, Rangoon (BMNH); 1 ♂, Upper Chindwin Dist. (BMNH); 1 ♀, Momeit, 2000 ft [600 m], vi.1890 (*Doherty*) (BMNH); 1 ♂, Lankhaung (*Swann*) (BMNH); 2 ♂, Htawgaw (*Swann*) (BMNH). **Vietnam**: 1 ♀, Haiphong (BMNH). **Thailand**: 10 ♂, 7 ♀, Bangkok, on *Oryza sativa*, 22.xii.1951–15.i.1952, 28.x.–23.xi.1952 (DA, Bangkok); 68 ♂, 91 ♀, Bangkok, at light, 1–31.xii.1968 (*Pholboon*) (DA, Bangkok); 3 ♂, 31 ♀, Bangkok (BMNH); 1 ♀, Khon Kaen, 22.xi.1955 (DA, Bangkok); 1 ♀, Pak Chong, Nakornrachsima, 16.x.1966 (DA, Bangkok); 5 ♀, Yala, 1.i.1964 (*Pholboon*) (DA, Bangkok); 1 ♀, Sukothai, 22.xi.1955 (DA, Bangkok); 1 ♂, Chiengmai, 6.ii.1928 (*Cockerell*) (BMNH); 1 ♂, Nonthaburi, 11.i.1951 (DA, Bangkok); 1 ♀, Thonburi, 1–13.x.1954 (DA, Bangkok); 1 ♂, 1 ♀, 20 km E. of Krabi, 21.ii.–10.iii.1962 (*Friedel*) (ZSBS, Munich); 2 ♂, Muak-Lek, Saraburi, 1000 ft [300 m], i. (*Fruhstorfer*) (BMNH). **West Malaysia**: 1 ♂, 2 ♀, Kuala Lumpur, 18.xii. (*Kloss*) (BMNH); 4 ♂, 2 ♀, Kuala Lumpur, at light, 22.iii.1941 (*Pendlebury*) (BMNH); 2 ♂, 4 ♀, Kuala Lumpur, at light, 31.i.1924 (BMNH); 2 ♂, Kuala Lumpur, at light, 23.iv.1931 (*Pendlebury*) (BMNH); 1 ♂, 15 ♀, Penang, i.1897 (*Curtis*) (BMNH); 1 ♀, Penang (*Ridley*) (BMNH); 1 ♂, Malacca (BMNH); 5 ♂, 2 ♀, Perak (BMNH); 2 ♀, Pahang, 20–23.viii.1935 (BMNH); 1 ♂, Pahang, 19.xi.1922 (*Pendlebury*) (BMNH); 1 ♀, Johore (*Ridley*) (BMNH); 1 ♂, Port Dickson, 12.i.1941 (BMNH); 1 ♀, Kedah State (*Cadman*) (BMNH). **Singapore**: 1 ♂, Kranji, 7.i.1923 (*Chasen*) (BMNH); 3 ♀, no precise locality (*Ridley*) (BMNH). **Sumatra**: 2 ♀, Padang, Mt Talang (BMNH); 16 ♀, Padang (BMNH); 1 ♀, Liwa, 900–1400 m (*Doherty*) (BMNH); 33 ♂, 8 ♀, Dempo, 4000 ft [1210 m], viii.1923 (*Brooks*) (BMNH); 12 ♀, Sandaran Agong, Korinchi, 2450 ft [740 m], v-vi.1914 (*Robinson & Kloss*) (BMNH); 1 ♀, Atjeh, Takengon, 22.vii.1914 (*Wagensveld*) (RNH, Leiden). **Java**: 2 ♂, Java (BMNH) (paralectotypes of *Schoenobius minutellus* Zeller); 1 ♂, 2 ♀, Bali (*Doherty*) (BMNH); 2 ♀, Lombok, Pringabaja, iv.1896 (*Fruhstorfer*) (BMNH); 2 ♀, Lombok (NR, Stockholm); 2 ♂, 5 ♀, Lombok, 1500 ft [450 m], iv.–v.1896 (*Everett*) (BMNH); 9 ♀, Djoenggo Ardijoeno, 4500 ft [1360 m], v.1934 (*Kalis*) (BMNH); 6 ♀, Bandung (BMNH); 1 ♀, Bangdung, 700 m, 12.v.1940 (*Olthof*) (RNH, Leiden); 1 ♀, Palabuan (BMNH); 1 ♂, 2 ♀, Soekaboemi (*Walsh*) (BMNH); 8 ♀, Nongkodjadjar, 4000 ft [1210 m], vi.1934 (*Kalis*) (BMNH); 16 ♀, Git-Git, 5000 ft [1500 m], v.1936 (*Kalis*) (BMNH); 2 ♀, Singalangoe, Tengger, 5000 ft [1500 m], iv.1934 (*Kalis*) (BMNH); 1 ♀, Sindanglaya, 26.ix.1920 (AMNH, New York); 1 ♀, Buitenzorg, i.1928 (*Burgeff*) (ZSBS, Munich); 1 ♀, Tijikadjang, Baudjorwangi, 7–10.iv.1939 (*Lieftinck*); 1 ♂, 2 ♀, Soekaboemie (MNHN, Paris); 1 ♂, 1 ♀, Bezoeki (*de Vaal*) (MNHN, Paris); 5 ♀, Radjamandala, 20–21.xii.1940 (*Olthof*) (RNH, Leiden); 3 ♀, no further data (BMNH); 4 ♀, no further data (NR, Stockholm). **Borneo**: 2 ♀, Pulo Laut, vi.1891 (*Doherty*) (BMNH); 13 ♂, 4 ♀, Pontianak (*Andre*) (BMNH); 2 ♀, Kinabalu, xii.1898–ii.1899 (*Waterstradt*) (BMNH); 3 ♀, Mt Marapok, Dent Province (BMNH); 2 ♀, Sarawak, 13.ii.1908 (*Meade Waldo*) (BMNH); 1 ♀, Mt Mulu, 1000–4000 ft [300–1210 m] (*Hose*) (BMNH); 4 ♀, Tambunan, 4–6.viii.1956 (BMNH); 5 ♀, Labuan, iii.1892 (*Everett*) (BMNH); 1 ♀, Lawas, iv.1892 (*Everett*) (BMNH); 1 ♀, Kuching, vii.1902 (BMNH); 1 ♀, Tinom (*Wahr*) (BMNH); 1 ♂, 1 ♀, no further data (BMNH). **Sumba**: 1 ♂, 1887 (*Doherty*) (BMNH). **Sulawesi**: 12 ♂, 6 ♀, Minahassa, Tomohon, 1.vi.–2.vii.1954 (*Alston*) (BMNH); 2 ♀, Menado (*Bracekel*) (BMNH). **Philippines**: 1 ♂, 9 ♀, Los Banos, Luzon, vii.1911 (*Wileman*) (BMNH); 3 ♂, Los Banos, Luzon (*Baker*) (NMNH, Washington); 14 ♂, 5 ♀, Klondyke, Benquet, Luzon, 800 ft [240 m], 18.xii.1911–24.v.1912 (*Wileman*) (BMNH); 22 ♂, 10 ♀, Manila, 4.i.–8.ii.1913 (*Wileman*) (BMNH); 1 ♀, Manila, 15.xi.1907 (*Betton*) (BMNH); 3 ♀, nr Manila (*Whitehead*) (BMNH); 1 ♂, Sapiangao, Benquet, Luzon, 5600 ft [1700 m], 16.xii.1912 (*Wileman*) (BMNH); 6 ♂, 2 ♀, Montalban, Rizal, Luzon (*Wileman*) (BMNH); 2 ♂, 6 ♀, Taytai, 10–18.ii.1907 (*Betton*) (BMNH); 2 ♂, Naga Hill, 5000–7000 ft [1500–2100 m], viii.–xi.1889 (*Doherty*) (BMNH); 4 ♂, 5 ♀, Palali, Benquet, Luzon, 2000 ft [600 m], 23–28.vii.1912, 3.vii.1913 (*Wileman*) (BMNH); 3 ♂, 1 ♀, Mt Makiling, Luzon (*Baker*) (BMNH); 1 ♂, Baquio, Benquet, Luzon, 5000 ft [1500 m], 16.vi.1913 (*Wileman*) (BMNH); 2 ♀, Zamboanga, Mindanao (AMNH, New York); 1 ♀, Limay, Luzon, 21.xi.1913 (ZSBS, Munich); 1 ♀, Luzon, 5000–6000 ft [1500–1800 m] (*Whitehead*) (BMNH): 1 ♀, no further data (BMNH). **Taiwan**: 5 ♂, 38 ♀, Kanshirei, vi.1904, vii.–ix.1908, iii.1909 (*Wileman*) (BMNH); 7 ♂, 38 ♀, Takow, viii.–ix.1904, vi.1905, vi.1906 (*Wileman*) (BMNH); 4 ♂, 8 ♀, Tainan, ii, iv, v, vi, 1904–07 (*Wileman*) (BMNH); 1 ♂, 2 ♀, Banshorio, 9.vi., 26.v.1906 (*Wileman*) (BMNH); 2 ♀, Koannania, vi.–viii.1906 (*Wileman*) (BMNH); 1 ♂, 1 ♀, Taihoku (*Shiraki*) (BMNH); 3 ♂, 13 ♀, vi.1904 (*Wileman*) (BMNH); 2 ♂, 3 ♀, Tainan (*Cheng*) (BMNH); 1 ♂, 3 ♀, Wanta nr Hori, Nan Tou Hsien, x.1965, iii.–v.1966 (CNC, Ottawa); 1 ♂, 5 ♀, no further data (BMNH). **Hong Kong**: 1 ♀, Sheung Shui, on *Oryza sativa*, 9.vii.1965 (*So*) (BMNH). **China**: 1 ♀ (BMNH) [abdomen missing] (paralectotype of *Chilo gratiosellus* Walker); 1 ♀, Shanghai (BMNH); 1 ♂, 1 ♀, Kwangtung, on *Oryza sativa*, 14.viii.1934 (*Chiu*) (BMNH); 3 ♀, Mt Omai, 4000 ft [1210 m], xii.1931 (BMNH); 1 ♀, Chu San I., vii.1892 (*Walker*) (BMNH); 1 ♀, Pagoda, ix.1899 (*de la Garde*) (BMNH); 5 ♀, Omei-Shan, 3500 ft [1060 m], vi.–vii.1890 (BMNH); 1 ♂, Youboi, Hainan, vi.1904 (BMNH); 1 ♂, Taipinshi, Hainan, viii.1905 (BMNH); 2 ♀, no further data (BMNH). **Japan**: 2 ♀, Iida San, Higo, Kyushu, 20.v.1895, 1899 (*Wileman*) (BMNH); 1 ♀, Osumi, Kyushu, 15.ix.1895 (*Wileman*) (BMNH); 1 ♂, Higo, Kyushu, 12.v.1899 (*Wileman*) (BMNH); 1 ♀, Amamiosima, Kagosima, 23.vii.1927 (CNC, Ottawa); 1 ♂, Amami, Kyushu, 23.vii.1959 (*Yukawa*) (CNC, Ottawa); 1 ♀, Osaka, Honshu, 2.vi.1959 (*Matuda*) (CNC, Ottawa).

Scirpophaga innotata (Walker, 1863)

(Figs 91, 92, 122, 183, 184, Map 8)

Tipanaea innotata Walker, 1863*b*: 523; Hampson, 1895: 914; 1896: 46 [as synonym of *Scirpophaga chrysorrhoa* Zeller]. Holotype ♀ [not ♂ as stated by Walker], BORNEO: Sarawak, Saunders' Coll (BMNH, Pyralidae genitalia slide no. 4029) [examined].



Map 12

Scirpophaga sericea Snellen, 1880: 79; Munroe et al., 1958: 84. Lectotype ♀, Sulawesi: Bonthain (RNH, Leiden), designated by Munroe et al. (1958: 84) [examined]. [Synonymized with *innotata* Walker by van der Goot, 1925.]

Scirpophaga innotata (Walker) van der Goot, 1925: 1–308; Jepson, 1954: 9.

Tryporyza innotata (Walker) Common, 1960: 340, figs 1D, 2B, 3E, 3F, 8F, pl. 2, figs 6, 7; Kapur, 1967: 6, 25.

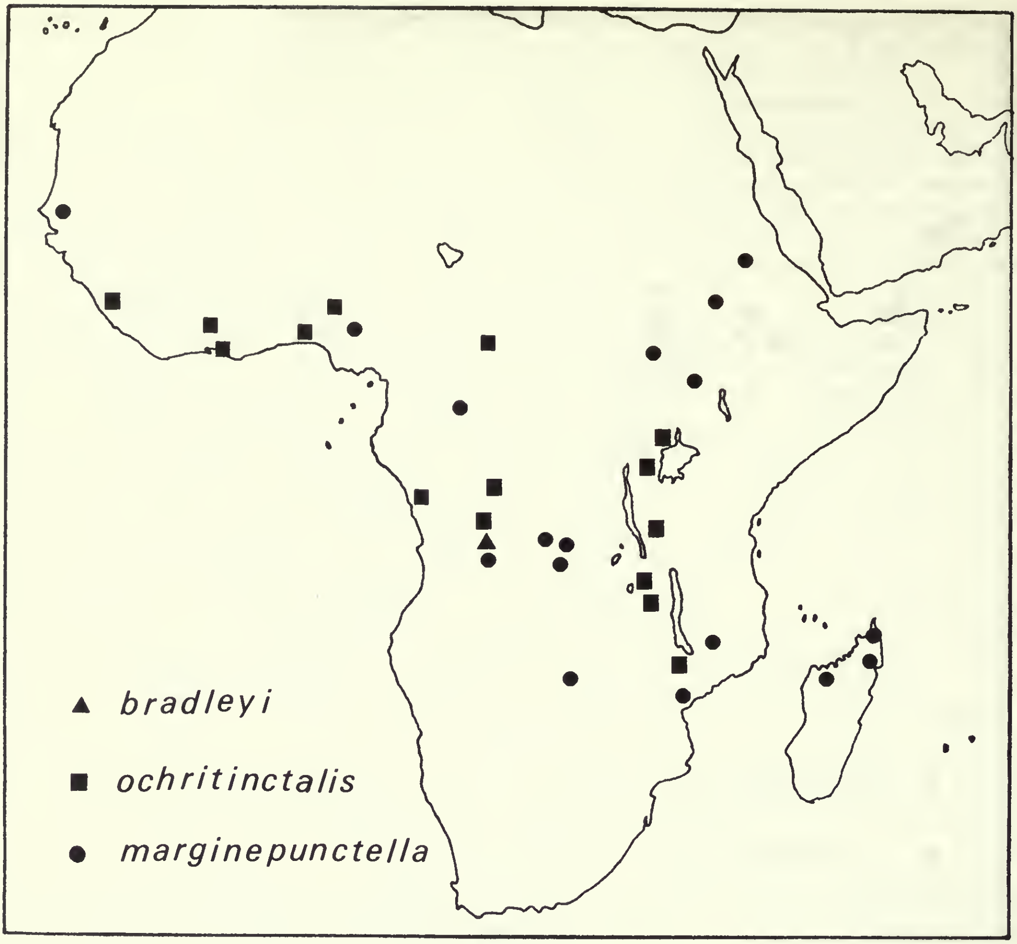
♂ (Fig. 183). 18–22 mm. Pale ochreous white. Length of labial palpus approximately 2 times diameter of compound eye. Forewing ochreous white, underside fuscous; hindwing white, costal half suffused with pale ochreous, stronger on underside.

♀ (Fig. 184). 22–33 mm. White. Forewing suffused with pale ochreous, underside white; hindwing white; frenulum double-bristled. Anal tuft white.

Genitalia ♂ (Figs 91, 92). As in *S. incertulas*, but the subteguminal process with a single spine.

Genitalia ♀ (Fig. 122). As in *S. incertulas*.

Remarks. The genitalia of both sexes of *S. innotata* are similar to those of *S. incertulas*; the only difference is in the subteguminal process of the male, which is a single spine in this species and a bifid spine in *S. incertulas*. The external characters of these two species are quite different; in *S. incertulas* the male has an ochreous forewing with markings, the female a yellow forewing with a dark fuscous spot. In *S. innotata* both the male and female have white forewings without markings.



Map 13

From the extensive material examined this species is apparently found only from eastern Asia to Australia. Carl (1962) mentioned *S. innotata* attacking rice in Pakistan, but this is probably a misidentification.

Biology. For host plants see p. 193.

Distribution. Borneo, Philippines, Sulawesi, Sumbawa, Sumba, Flores, Timor, New Guinea, Australia.

Material examined

Borneo: 1 ♂, 1 ♀, Pulo Laut (*Doherty*) (BMNH); 1 ♂, 1 ♀, Labuan, 31.i., 12.ii.1963 (*Barlow*) (BMNH); 1 ♂, Likong, on *Oryza sativa*, 13.ix.1967 (BMNH); 1 ♂, Kapit, on *Oryza sativa*, 1.iii.1965 (*Rothschild*) (BMNH); 3 ♀, Kuching, in rice-fields, 3.viii–23.xii.1961 (*Teo*) (BMNH); 2 ♀, Kuching, 3.ix., 3.xi.1962 (BMNH); 1 ♀, 80 mls [129 km] N. Pontinak, iv.1909 (BMNH); 6 ♂, 2 ♀, Sarawak, on *Oryza sativa* (BMNH); 1 ♂, Simanggang, on *Oryza sativa*, 22.i.1962 (*Wan*) (BMNH); 1 ♀, Trusan, 16.ix.1962 (BMNH). **Philippines**: 1 ♂, 2 ♀, Iloilo, 6.ix.1928 (*Sison*) (NMNH, Washington); 2 ♂, Victorias, Occ. Negros, 19, 22.xii.1927 (*Uichanco*) (NMNH, Washington); 1 ♀, Victorias, Occ. Negros, on *Saccharum officinarum*, 28.x.1927 (NMNH, Washington); 1 ♀, no further data (BMNH). **Sulawesi**: 1 ♀, Bonthain (*Doherty*) (BMNH); 2 ♂, 9 ♀, Tolitoli, xi., xii.1895 (*Fruhstorfer*) (BMNH); 1 ♀, Minahassa, 8.vi.1954 (*Alston*) (BMNH); 1 ♂, Maros, 1 ♀, Tjamba (*Doherty*) (BMNH); 1 ♀, Maros, 13.vii.1910 (BMNH); 2 ♂, Samanga, xi.1895 (*Fruhstorfer*) (BMNH); 1 ♂, 2 ♀, Parepare, 27–28.viii.1904 (UM, Oxford). **Sumbawa**: 1 ♂, 1887

(*Doherty*) (BMNH). **Sumba**: 2 ♀, 1887 (*Doherty*) (BMNH). **Flores**: 1 ♀, Koelawi, Paloë I., 3100 ft [940 m], iii.1907 (*Kalis*) (BMNH). **Timor**: 2 ♂, 2 ♀, Dili, v.1892 (*Doherty*) (BMNH). **New Guinea**: 2 ♂, Digoel R., 1924 (*Vertenten*) (ZM, Amsterdam). **Australia**: 1 ♂, Derby (*Turner*) (BMNH); 1 ♂, 1 ♀, Humpty Doo, 3.iv.1959 (*Common*) (BMNH); 1 ♀, Port Darwin, 1910 (*Dodd*) (BMNH); 1 ♀, Percy I., 1910 (*Lathy*) (BMNH).

The *gotoi*-group

Forewing with vein R_1 anastomosed with *Sc*. Frenulum a single bristle in both sexes.

GENITALIA ♂. Uncus and gnathos long and slender; tegumen with sclerotized thickening ×-shaped; subteguminal process lobe-like; aedeagus slender, vesica with minute spines.

GENITALIA ♀. Ductus bursae sclerotized throughout, section between ostium bursae and ductus seminalis constricted; corpus bursae with dense spines.

The *gotoi*-group consists of one species, *S. gotoi*. The ×-shaped dorsal sclerotized thickening of the tegumen and the lobe-like subteguminal process are similar to those in the *occidentella*-group, but in the *gotoi*-group the anellus is lined with minute spines not as strongly sclerotized as those in the *occidentella*-group. In the female genitalia the ductus bursae is sclerotized throughout as in the *praelata*-group but the 8th tergal plate is not produced ventrolaterally. Externally vein R_1 in the *gotoi*-group anastomoses with *Sc* but in the *praelata*-group they are separate.

Scirpophaga gotoi sp. n.

(Figs 67, 68, 112, 185, 186, Map 9)

♂ (Fig. 185). 23–24 mm. Ochreous yellow. Length of labial palpus approximately 3 times diameter of compound eye. Forewing shining ochreous yellow with dark fuscous spot at lower angle of cell, R_1 usually anastomosed with *Sc*, underside fuscous; hindwing ochreous yellow, underside suffused with fuscous in costal half.

♀ (Fig. 186). 26–30 mm. As in ♂ but underside of wings not suffused with fuscous; frenulum single-bristled. Anal tuft ochreous yellow.

GENITALIA ♂ (Figs 67, 68). Tegumen with dorsal sclerotized thickening ×-shaped; subteguminal process lobe-like; aedeagus slender; vesica with minute spines.

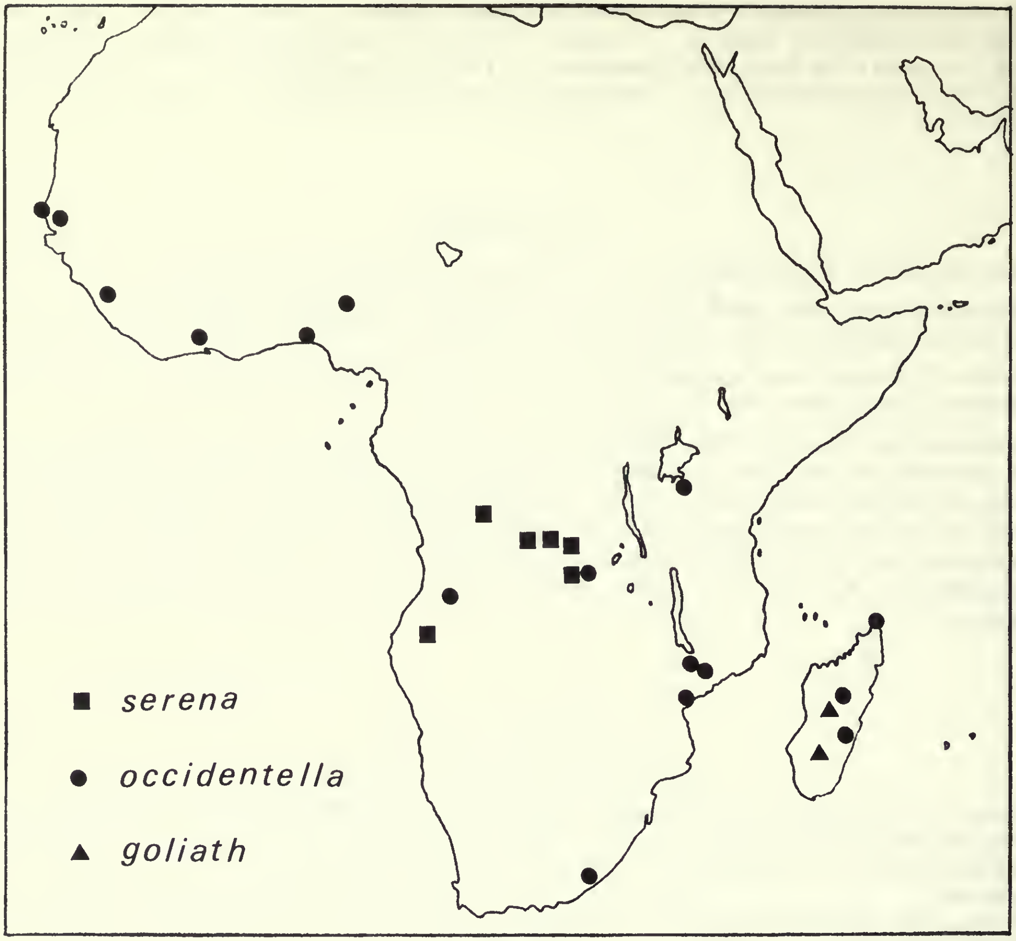
GENITALIA ♀ (Fig. 112). Ostium bursae membranous; ductus bursae wholly sclerotized, section between ostium bursae and ductus seminalis constricted, gradually dilating towards corpus bursae; corpus bursae with dense spines.

REMARKS. Both sexes of this species are very similar to the female of *S. incertulas* in coloration and in the presence of the spot in the forewing, but in *S. gotoi* the wings are more shining. *S. gotoi* also differs in having vein R_1 anastomosing with *Sc* and the frenulum in the female is of the one-bristled type, while in *S. incertulas* vein R_1 is usually not anastomosed with *Sc* and the frenulum in the female consists of two bristles. In the genitalia these two species are quite distinct. In *S. gotoi* the male has the tegumen with the dorsal sclerotized thickening ×-shaped and a lobe-like subteguminal process. In the female the ostium bursae is not wrinkled and the ductus bursae is sclerotized throughout the duct, while in *S. incertulas* the ostium bursae is wrinkled and the ductus bursae is membranous.

S. incertulas has been studied intensively in many rice-growing countries in Asia, including Japan. Because of the similarity between *S. gotoi* and the female of *S. incertulas*, *S. gotoi* should not be overlooked.

BIOLOGY. Unknown.

DISTRIBUTION. Japan, China.



Map 14

MATERIAL EXAMINED

Holotype ♂, **Japan**: Niitsu City [37°48′N, 139°09′E], Niigata Pref. (*S. Sakurai*) (CNC, Ottawa).

Paratypes. **Japan**: 1 ♀, data as holotype (CNC, Ottawa); 1 ♂, same data as holotype, 15.vii.1963 (CNC, Ottawa); 1 ♀, Niigata University, 30.vii.1962 [Japanese label] (CNC, Ottawa).

Non-paratypic material. **China**: 1 ♀, Lungtan, nr Nanking. Prov. Kiangsu, 27.vii.1933 (*Höne*) (MAK, Bonn); 1 ♀, same locality, 28.viii.1933 (*Höne*) (LN, Karlsruhe).

This species is named after Mr H. E. Goto, Imperial College of Science and Technology, London.

The *whalleyi*-group

Forewing with vein R_1 anastomosed with *Sc*. Frenulum in male a single bristle, in female with double fused bristle.

GENITALIA ♂. Uncus and gnathos long, slender, tegumen with dorsal sclerotized thickening somewhat triangular, subteguminal process membranous; aedeagus slender, vesica with a group of curved spined cornuti.

GENITALIA ♀. Ductus seminalis arising from ductus bursae near ostium bursae; corpus bursae membranous.

The *whalleyi*-group, consisting of one species, differs from the others by the membranous subteguminal process in the male genitalia.

***Scirpophaga whalleyi* sp. n.**

(Figs 93, 94, 124, 187, 188, Map 5)

♂ (Fig. 187). 19–21 mm. Ochreous yellow. Labial palpus suffused with yellow, in length approximately 2 times diameter of compound eye. Forewing yellow, vein R_1 anastomosed with *Sc*, underside pale ochreous; hindwing white with pale yellow suffusion in costal half.

♀ (Fig. 188). 21–27 mm. Coloration as in male but paler and underside of forewing not suffused with ochreous; frenulum double-fused bristled. Anal tuft pale yellowish white.

GENITALIA ♂ (Figs 93, 94). Uncus and gnathos long slender; tegumen with dorsal sclerotized thickening somewhat triangular; subteguminal process membranous with sclerotized base; aedeagus slender, vesica with small spines, a group of curved-spined cornuti present.

GENITALIA ♀ (Fig. 124). Ostium bursae membranous; lined with small spines; ductus seminalis and ductus bursae strongly sclerotized near ostium bursae, otherwise membranous; corpus bursae membranous.

REMARKS. In both sexes, *S. whalleyi* is similar to the female of *S. incertulas* except that the dark fuscous spot on the forewing, which is present in *S. incertulas*, is absent in *S. whalleyi*. In the female of *S. incertulas* vein R_1 usually does not anastomose with *Sc* and the frenulum consists of two bristles, while in *S. whalleyi*, R_1 anastomoses with *Sc* and the frenulum consists of a double-fused bristle. The male genitalia are also similar to those of *S. incertulas*, but the subteguminal process is membranous, and the cornuti in the vesica of the aedeagus consist of a group of curved spines instead of the two unequal spines found in *S. incertulas*. The female genitalia of *S. whalleyi* are quite different from those of *S. incertulas* in that the ostium bursae is not wrinkled and the corpus bursae is membranous.

BIOLOGY. Unknown.

DISTRIBUTION. Sri Lanka, India.

MATERIAL EXAMINED

Holotype ♂, **Sri Lanka**: 'Dambool [Dambulla, 7°51′N, 80°40′E], Ceylan' (BMNH, Pyralidae genitalia slide no. 11015).

Paratypes. **Sri Lanka**: 1 ♀, same data as holotype (BMNH); 1 ♂, Dambool [Dambulla], xi.1902, Mackwood Coll. (BMNH); 2 ♂, 1 ♀, Habarana [Habarane], xi.1902, Mackwood Coll. (BMNH); 1 ♀, Apura, xii.1902, Mackwood Coll. (BMNH); 4 ♀, Puttalam (BMNH); 1 ♀, Hambanto-ta (BMNH); 1 ♀, no precise locality (BMNH); 2 ♀, no precise locality, Paravicini Coll. (BMNH).

Non-paratypic material. **India**: 1 ♂, 2 ♀, Calcutta, 1858 (*Atkinson*) (BMNH); 1 ♀, Madras, vii.1891 (BMNH); 1 ♀, Nudangalam, Madras, in rice-field, 30.x.1962 (BMNH).

This species is named after Dr P. E. S. Whalley, British Museum (Natural History), London.

References

Aurivillius, C. 1898. Bemerkungen zu den von J. Chr. Fabricius aus Dänischen Sammlungen beschriebenen Lepidopteren. *Ent. Tidskr.* **1898** (1897): 139–174.

Avasthy, P. N. 1969. The top borer of sugar cane, *Scirpophaga nivella* (F.). *In: Pests of sugar cane* pp. 188–205. Amsterdam.

Banerjee, S. N. & Pramanik, L. M. 1967. The lepidopterous stalk borers of rice and their life cycles in the tropics. *In: The major insect pests of the rice plant* pp. 103–124. Proceedings of a symposium at the International Rice Research Institute, September, 1964.

Błeszyński, S. 1965. Crambinae. *Microlepidoptera Palaearctica* **1**. 533 pp., 133 pls. Vienna.

Box, H. E. 1953. *List of sugar cane insects.* 101 pp. London.

Butani, D. K. 1970. Systematic position of sugar cane top borer in India. *Labdev J. Sci. Tech.* **8**(B) 3: 167–170.

Butler, A. G. 1879. Description of new species of Lepidoptera from Japan. *Ann. Mag. nat. Hist.* (5) **4**: 349–374, 437–457.

—— 1880. On a second collection of Lepidoptera made in Formosa by H. E. Hobson, Esq. *Proc. zool. Soc. London.* **1880**: 666–691.

Caradja, A. 1925. Ueber Chinas Pyraliden, Tortriciden, Tineiden nebst kurze Betrachtungen, zu denen das Studium dieser Fauna Veranlassung gibt. *Memle Sect. stiint. Acad. rom.* (3) **3** (7): 1–127, 2 pls.

—— 1932. Dritter Beitrag zur Kleinfalterfauna Chinas nebst kurzer Zusammenfassung der bisherigen biogeographischen Ergebnisse. *Bull. Sect. scient. Acad. roum.* **15** (7, 8): 111–124, 203–212.

—— 1938*a*. Ueber eine kleine Mikrolepidopterenausbeute aus Manciukuo und Transbaikalien. *Dt. ent. Z. Iris* **52**: 90–92.

—— 1938*b*. Materialien zu einer Microlepidopteren-Fauna Nord-Fukiens. *Stettin. ent. Ztg* **99**: 253–257.

Carl, K. 1962. Graminaceous moth-borers in west Pakistan. *Tech. Bull. Commonw. Inst. biol. Control* **2**: 29–76.

Chatterjee, D. 1951. Note on the origin and distribution of wild and cultivated rices. *Indian J. Genet. pl. Breed.* **11**(1): 18–21.

Common, I. F. B. 1960. A revision of the Australian stem borers hitherto referred to *Schoenobius* and *Scirpophaga* (Lepidoptera: Pyralidae, Schoenobiinae). *Aust. J. Zool.* **8**: 307–347, 8 figs, 2 pls.

—— 1970. Lepidoptera. *In: The insects of Australia.* 1029 pp. Melbourne.

Darlington, P. J. 1957. *Zoogeography, the geographical distribution of animals.* 675 pp. New York.

Duponchel, P. A. J. 1836. *In* Godart, J. B., *Histoire naturelle des Lépidoptères ou papillons de France* **10** (7): 1–387, pls 267–286. Paris.

—— [1846] *Catalogue méthodique des Lépidoptères d'Europe.* 523 pp. Paris.

Dyar, A. G. 1903. A list of north American Lepidoptera and key to the literature of this order of insects. *Bull. U.S. natn. Mus.* **52.** 723 pp.

——1913. Notice of volume ii. no. 4. of Barnes and McDunnough's "Contributions to the Natural History of the Lepidoptera of North America". *Insecutor Inscit. menstr.* **1**: 102–106.

Fabricius, J. C. 1974. *Entomologia systematica emendata et aucta.* 3(2). 349 pp. Hafniae.

—— 1798. *Entomologia systematica emendata et aucta.* Supplementum. 572 pp. Hafniae.

Fletcher, T. B. 1917. *Rep. Proc. 2nd ent. Meet. Pusa.* 340 pp.

—— 1921. Annotated list of Indian crop-pests. *Bull. agric. Res. Inst. Pusa* **100**: 1–246.

—— 1923. Note on identification of *Siga incertellus,* Wlk. *Mem. Dept. Agric. India* **7**: 276–278.

—— 1928. Report of the Imperial Entomologist. *Scient. Rep. agric. Res. Inst. Pusa 1926–27.* **1928**: 56–67, 10 pls.

Fletcher, T. B. & Ghosh, C. C. 1920. Borers in sugar cane, rice, etc. *Rep. Proc. 3rd ent. Meet. Pusa* **1**: 354–417.

Forbes, W. T. M. 1923. Lepidoptera of New York and neighbouring states. Primitive forms, Microlepidoptera, Pyraloids, Bombyces. *Mem. Cornell Univ. agric. Exp. Stn* **68.** 729 pp.

—— 1926. The relationships of some aberrant Pyralids (Lep.). *Jl N.Y. ent. Soc.* **34**: 331–339, pl. 25.

Freyer, C. F. 1833. *Neuere Beiträge zur Schmetterlingskunde.* 182 pp., pls 1–96. Augsburg.

—— 1836. *Neuere Beiträge zur Schmetterlingskunde.* 161 pp., pls 97–192. Augsburg.

Gressitt, J. L. 1956. Some distribution patterns of Pacific Island faunae. *Syst. Zool.* **5**: 11–32, 47; 9 maps.

—— 1958. Zoogeography of insects. *A. Rev. Ent.* **3**: 207–230.

Grist, D. H. 1965. *Rice.* (Ed. 4) 548 pp. London.

Grist, D. H. & Lever, R. J. A. W. 1969. *Pests of rice.* 520 pp. London.

Guenée, A. 1845. Essai sur une nouvelle classification des Microlépidoptères. *Annls Soc. ent. Fr.* (2) **3**: 297–344.

—— 1875. *Statistique scientifique d'Eure-et-Loire.* Lépidoptères. 298 pp. Chartres.

Gupta, V. K. 1962. Taxonomy, zoogeography, and evolution of Indo-Australian *Theronia* (Hymenoptera: Ichneumonidae). *Pacif. Insects Monogr.* **4**: 1–142.

Hampson, C. F. 1893. The Macrolepidoptera Heterocera of Ceylon. *Illustrations of typical specimens of Lepidoptera Heterocera in the collection of the British Museum.* **9.** 182 pp., pls 157–176. London.

—— 1895. On the classification of the Schoenobiinae and Crambinae, two subfamilies of moths of the family Pyralidae. *Proc. zool. Soc. Lond.* **1895**: 897–974.

—— 1896. Moths. *Fauna Br. India* **4.** 594+27 pp. London.

—— 1903. The moths of India. Supplementary paper to the volumes in "The fauna of British India". *J. Bombay nat. Hist. Soc.* **15**: 19–37.

—— 1919*a*. Descriptions of new Pyralidae of the sub-families Crambinae and Siginae. *Ann. Mag. nat. Hist.* (9) **3**: 275–292, 437–457, 533–547.

—— 1919*b*. Descriptions of new Pyralidae of the sub-families Crambinae and Siginae. *Ann. Mag. nat. Hist.* (9) **4**: 53–68, 137–154, 305–326.

Heinemann, H. von. 1865. *Die Schmetterlinge Deutschlands und der Schweiz* (2) **1** (2). 214 pp. Braunschweig.

Heinrich, C. 1937. Moths of the genus *Rupela* (Pyralididae: Schoenobiinae). *Proc. U.S. natn. Mus.* **84**: 355–388.

Herrich-Schäffer, G. A. W. 1848–1851. *Systematische Bearbeitung der Schmetterlinge von Europa* **4.** 288 pp. Regensburg.

Horn, W. & Kahle, I. 1936. Über entomologische Sammlungen (Ein Beitrag zur Geschichte der Entomo-Museologie). *Ent. Beih. Berl.-Dahlem* **3**: 161–296.

Hübner, J. 1790. *Beiträge zur Geschichte der Schmetterlinge* **2.** 134 pp. 16 pls. Augsburg.

—— 1796. *Sammlung europäischer Schmetterlinge* **8.** Tineae. 70 pp., 34 pls. Augsburg.

—— [1800]–[1838]. *Sammlung europäischer Schmetterlinge* **3.** Bombyces. 83 pls. Augsburg.

—— 1816–[1826]. *Verzeichniss bekannter Schmettlinge.* 432+72 pp. Augsburg.

Jepson, W. F. 1954. *A critical review of the world literature on the lepidopterous stalk borers of tropical Graminaceous crops.* 127 pp. London.

Joannis, J. de 1927. Pyralidae d'Afrique australe principalement du district de Lourenço-Marquès. *Bull. Soc. lépidopt. Genève* **5**: 181–256.

—— 1929. Lépidoptères Hétérocères du Tonkin. *Annls Soc. ent. Fr.* **98**: 559–833.

Jordan, K. 1923. On a sensory organ found on the head of many Lepidoptera. *Novit. zool.* **30**: 155–158.

Kapur, A. P. 1967. Taxonomy of the rice stem borers. *In: The major insect pests of the rice plant.* Proceedings of a symposium at the International Rice Research Institute, September, 1964, pp. 3–43.

Kiritani, K. & Iwao, S. 1967. The biology and life cycle of *Chilo suppressalis* (Walker) and *Tryporyza* (*Schoenobius*) *incertulas* (Walker) in temperate-climate areas. *In: The major insect pests of the rice plant.* Proceedings of a symposium at the International Rice Research Institute, September, 1964. pp. 45–101.

Kostrowicki, A. S. 1969. *Geography of the Palaearctic Papilionoidea* (*Lepidoptera*). 380 pp. Kraków.

Kratochvil, F. 1956. Rice moves northward. *Wld Crops* **8**: 146–147.

Lange, W. H. 1956. A generic revision of the aquatic moths of North America (Lepidoptera: Pyralidae, Nymphulinae). *Wasmann J. Biol.* **14**: 59–144.

Leech, J. H. 1901. Lepidoptera Heterocera from China, Japan, and Korea. *Trans. ent. Soc. Lond.* **1901**: 385–514.

Logothetis, C. 1950. *Review of available information on some insects affecting the rice crop in southeast Asia.* 25+4 pp., multigraph. Washington, D.C.

Marion, H. & Viette, P. 1953. Descriptions de deux nouvelles Pyrales malgaches (Lep. Pyralididae). *Bull. Soc. ent. Fr.* **58**: 39–42, 4 figs.

Marumo, N. 1934. Studies on rice borers. II. Classification of the subfamily Siginae in Japan. *Minst. agric. for. Japan dept. Agric.* **90.** 29+1 pp., 5 pls. [In Japanese with English summary.]

Martin, E. L. 1958. Notes on some rice stem borers (Lepidoptera: Pyralidae), with the description of a new species of *Chilo* Zincken. *Bull. ent. Res.* **49**: 187–191, pl. 6.

Meyrick, E. 1878. Descriptions of Australian Micro-Lepidoptera. *Proc. Linn. Soc. Lond.* **3**: 175–216.

—— 1882. Descriptions of Australian Micro-Lepidoptera. *Proc. Linn. Soc. Lond.* **7**: 148–202.

—— 1885. On the classification of the Australian Pyralidina. *Trans. ent. Soc. Lond.* **1885**: 421–456.

—— 1886. Descriptions of Lepidoptera from the south Pacific. *Trans. ent. Soc. Lond.* **1886**: 189–296.

—— 1887. On Pyralidina from Australia and the south Pacific. *Trans. ent. Soc. Lond.* **1887**: 185–268.

—— 1889. On some Lepidoptera from New Guinea. *Trans. ent. Soc. Lond.* **1889**: 455–522.

—— 1890. On the classification of the Pyralidina of the European fauna. *Trans. ent. Soc. Lond.* **1890**: 429–492.

——.1894. On Pyralidina from the Malay Archipelago. *Trans. ent. Soc. Lond.* **1894**: 455–480.

—— 1930–1936. *Exotic Microlepidoptera* **4.** 642 pp. London.

Moore, F. 1867. On the lepidopterous insects of Bengal. *Proc. zool. Soc. Lond.* **1867**: 612–686, pls 32, 33.

—— 1884–87. *The Lepidoptera of Ceylon* **3.** 578 pp., 215 pls. London.

—— 1888. *Descriptions of new Indian lepidopterous insects from the collection of the late Mr. M. S. Atkinson, M.A. F.L.S.* Heterocera pp. 199–299, 7 pls. London.

Moritsugu, A. 1931. Studies on the top-borer attacking the sugar cane in Formosa. [In Japanese.] *Rep. Dept. Agric. Govt. Res. Inst. Formosa* **50.** 56 pp., 3 pls. [English abstract. *Rev. appl. Ent.* (A) **19**: 513.]

Munroe, E. G. 1956. Hampson's Schoenobiinae (Lepidoptera: Pyralidae). *Proc. 10th Int. Congr. Ent.* **1**: 301–302.

Munroe, E. G., Diakonoff, A. & Martin, E. L. 1958. Catalogue of Snellen's types of Pyralidae, with selections of lectotypes. *Tijdschr. Ent.* **101**: 65–88.

Nagaraja, H. 1972. Further evidence to support inclusion of the Oriental sugarcane top borer *Scirpophaga nivella* (Fab.) in the genus *Tryporyza* Common. *Oriental Insects* **6**: 507–511.

Ragonot, E. L. 1891. Essai sur la classification des Pyralites. *Annls Soc. ent. Fr.* (6) **10**: 435–546.

Rebel, H. 1901. *In* Staudinger, O. & Rebel, H., *Catalog der Lepidopteren des palaearctischen Faunengebietes.* 368 pp. Berlin.

Rehfous, M. 1906. Note sur *Scirpophaga praelata* Scop. *Bull. Soc. Lépidopt. Genève* **1**: 154–160.

Rossi, P. 1790. *Fauna Etrusca, sistens insectae, quae in provinciis Florentina et Pisana praesertim collegit* **2.** 348 pp. Liburni.

Schawerda, K. 1922. Ussuriensia. *Z. öst. EntVer.* **7**: 10–11.

Schultze, W. 1908. New and little-known Lepidoptera of the Philippines Islands. *Philipp. J. Sci.* (A) **3**: 27–39, 1 pl.

Scopoli, J. A. 1763. *Entomologia carniolica, exhibens Insecta Carnioliae indigena.* 420 pp., 43 pls. Vindobonae.

Shibuya, J. 1928. The systematic study on the Formosan Pyralidae. *J. Fac. Agric. Hokkaido Univ.* **22** (1): 300 pp., pls 1–9.

—— 1931. *Insect Wld* **35**: 365–371. [In Japanese.]

Shiraki, T. 1917. Paddy borer, *Schoenobius incertellus* Wlk. *Spec. Rep. Agric. exp. Stn Taihoku, Formosa* No. 15: 256 pp., 22 pls, 1 map.

Shroff, K. D. 1920. A list of the pests of cereals in Burma. *Rep. Proc. 3rd ent. Meet. Pusa* **1**: 341–343.

Snellen, P. C. T. 1880. Lepidoptera. *Midden-Sumatra* **4** (1) 8: 1–92, 5 pls.

—— 1890. Aanteekeningen over Lepidoptera schadelijk voor het suikerriet. *Meded. Proefstn SuikRiet W. Java 'Kagok'.* **1890**: 94.

—— 1891. Aanteekeningen over Lepidoptera schadelijk voor het suikerriet. *Tijdschr. Ent.* **34**: 230–356.

Strand, E. 1918. H. Sauter's Formosa-Ausbeute: Pyralididae, Subfam. Galleriinae, Crambinae, Schoenobiinae, Anerastiinae und Phycitinae. *Stettin. ent. Ztg* **79**: 248–276.

Szent-Ivány, J. & Uhrik-Mészáros, T. 1942. A Pyralididae- Csalad (Lepidopt.) elterjedese a Karpati Medenceben. *Annls hist-nat. Mus. natn. hung.* (Zool.) **35**: 109–196, pl. 4.

Treitschke, F. 1832. *Die Schmetterlinge von Europa* **9** (1). 262 pp. Leipzig.

—— 1835. *Die Schmetterlinge von Europa* **10** (2). 340 pp. Leipzig.

Turner, J. 1922. Studies in Australian Lepidoptera. *Proc. R. Soc. Vict.* **35**: 26–62.

—— 1937. New Australian Pyraloidea (Lepidoptera). *Proc. R. Soc. Qd* **48**: 61–88.

Van der Goot, P. 1925. Levenswijze en bestrijding van den Witten Rijstboorder op Java. *Meded. Inst. PlZiekt. Buitenz.* **66.** 308 pp.

Walker, F. 1863*a*. Crambites & Tortricites. *List of the specimens of lepidopterous insects in the collection of the British Museum.* **27.** 286 pp. London.

—— 1863*b*. Tortricites & Tineites. *List of the specimens of lepidopterous insects in the collection of the British Museum.* **28**: 287–561. London.

—— 1864. Tineites. *List of the specimens of lepidopterous insects in the collection of the British Museum.* **30**: 837–1096. London.

Wallace, A. R. 1876. *The geographical distribution of animals* **1.** 503 pp. London.

Watson, A. 1967. A survey of the extra-Ethiopian Oretinae (Lepidoptera: Drepanidae). *Bull. Br. Mus. nat. Hist.* (Ent) **19**: 151–221, 9 pls.

Werneburg, A. 1864. *Beiträge zur Schmetterlingskunde* **2.** 347 pp. Erfurt.

Whalley, P. E. S. 1971. The Thyrididae (Lepidoptera) of Africa and its islands. A taxonomic and zoogeographic study. *Bull. Br. Mus. nat. Hist.* (Ent.) Suppl. 17. 198 pp., 68 pls.

Wileman, A. E. 1911. New and unrecorded species of Lepidoptera Heterocera from Japan. *Trans. ent. Soc. Lond.* **1911**: 189–407, pls 30, 31.

Wileman, A. E. & South, R. 1918. New species of Pyralidae from Formosa. *Entomologist* **51**: 217–219.

Wocke, M. 1871. In Staudinger, O., *Catalog der Lepidopteren des europaeischen Faunengebiets.* 426 pp. Dresden.

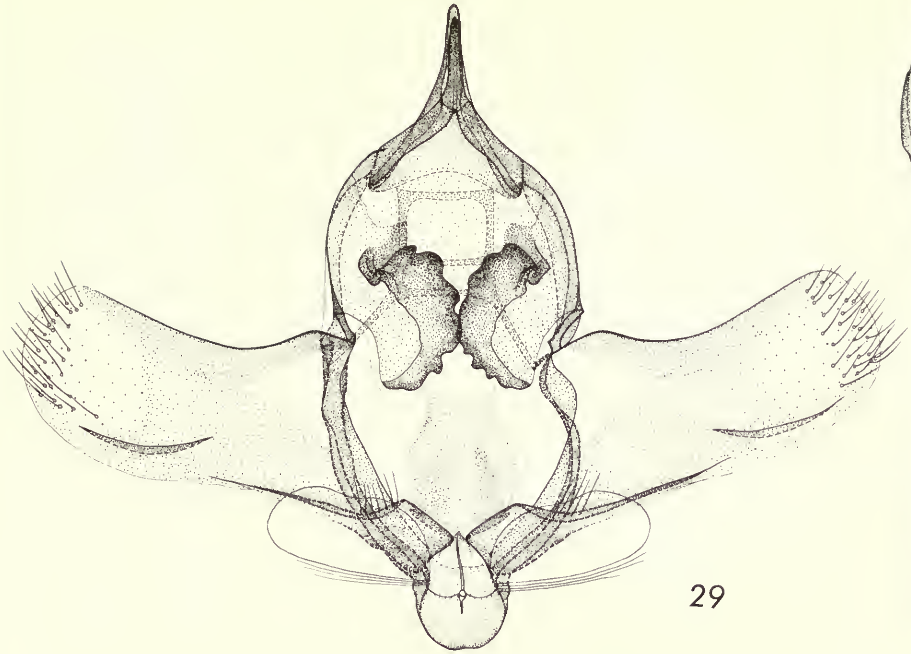
Zeller, P. C. 1839. Versuch einer naturgemässen Eintheilung der Schaben. *Isis, Leipzig* **23**: 167: 171.

—— 1863. *Chilonidarum et Crambidarum genera et species.* 56 pp. Berlin.

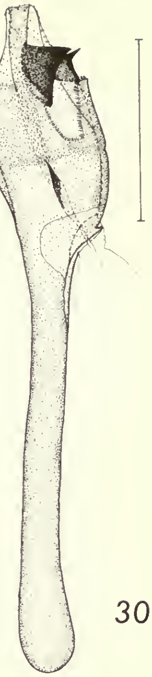
Zeuner, F. E. 1941. Geology, climate and faunal distribution in the Malay Archipelago. *Proc. ent. Soc. Lond.* (A) **16**: 117–123.

—— 1943. Studies in the systematics of *Troides* (Lepidoptera, Papilionidae) and its allies; distribution and phylogeny in relation to the geological history of the Australian Archipelago. *Trans. zool. Soc. Lond.* **25**: 107–184.

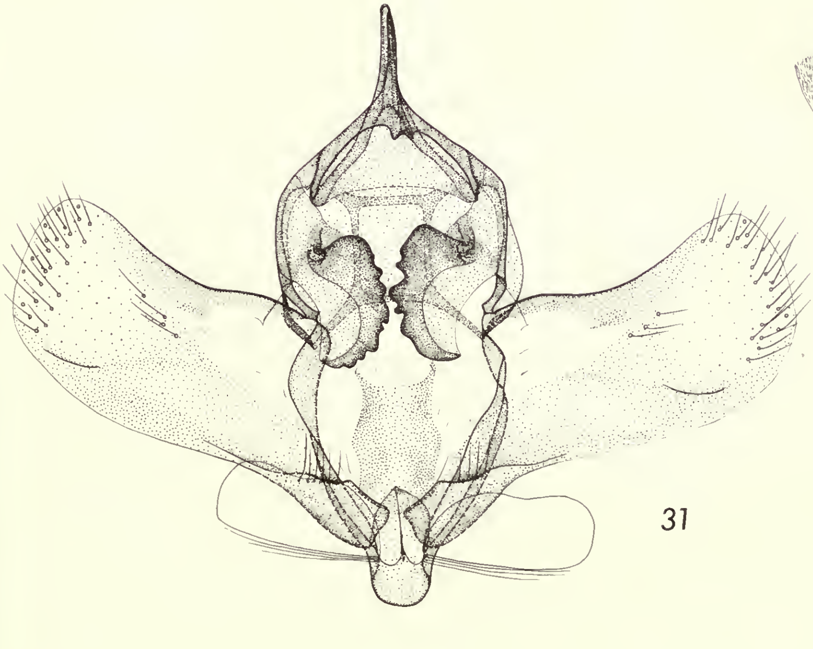
Zimsen, E. 1964. *The type material of I. C. Fabricius.* 656 pp. Munksgaard.



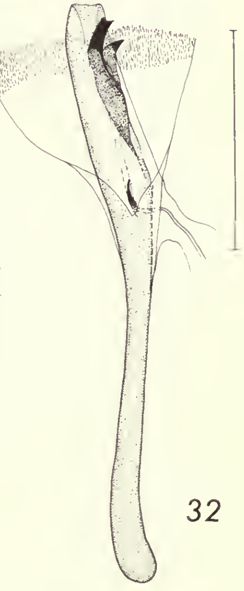
29



30

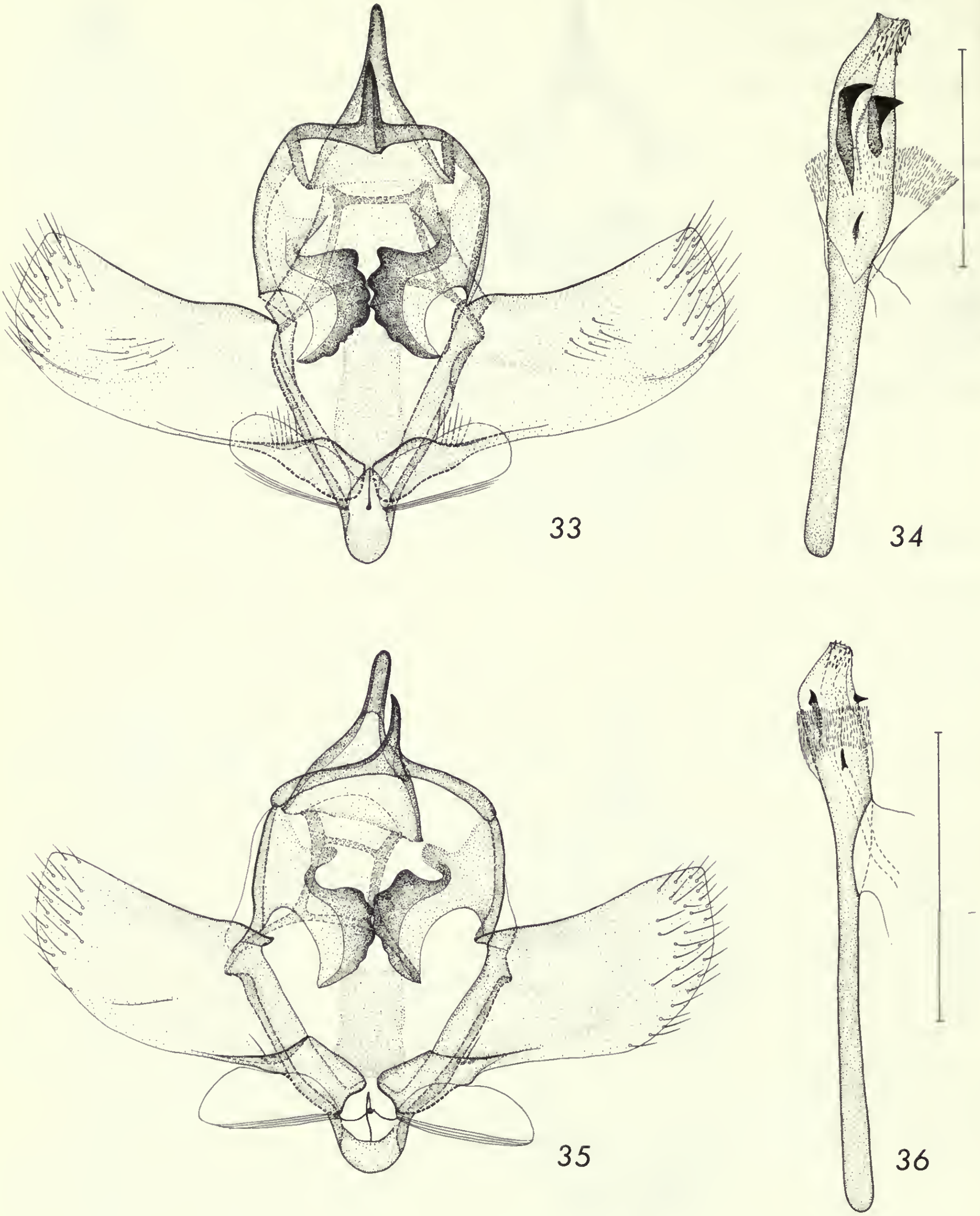


31

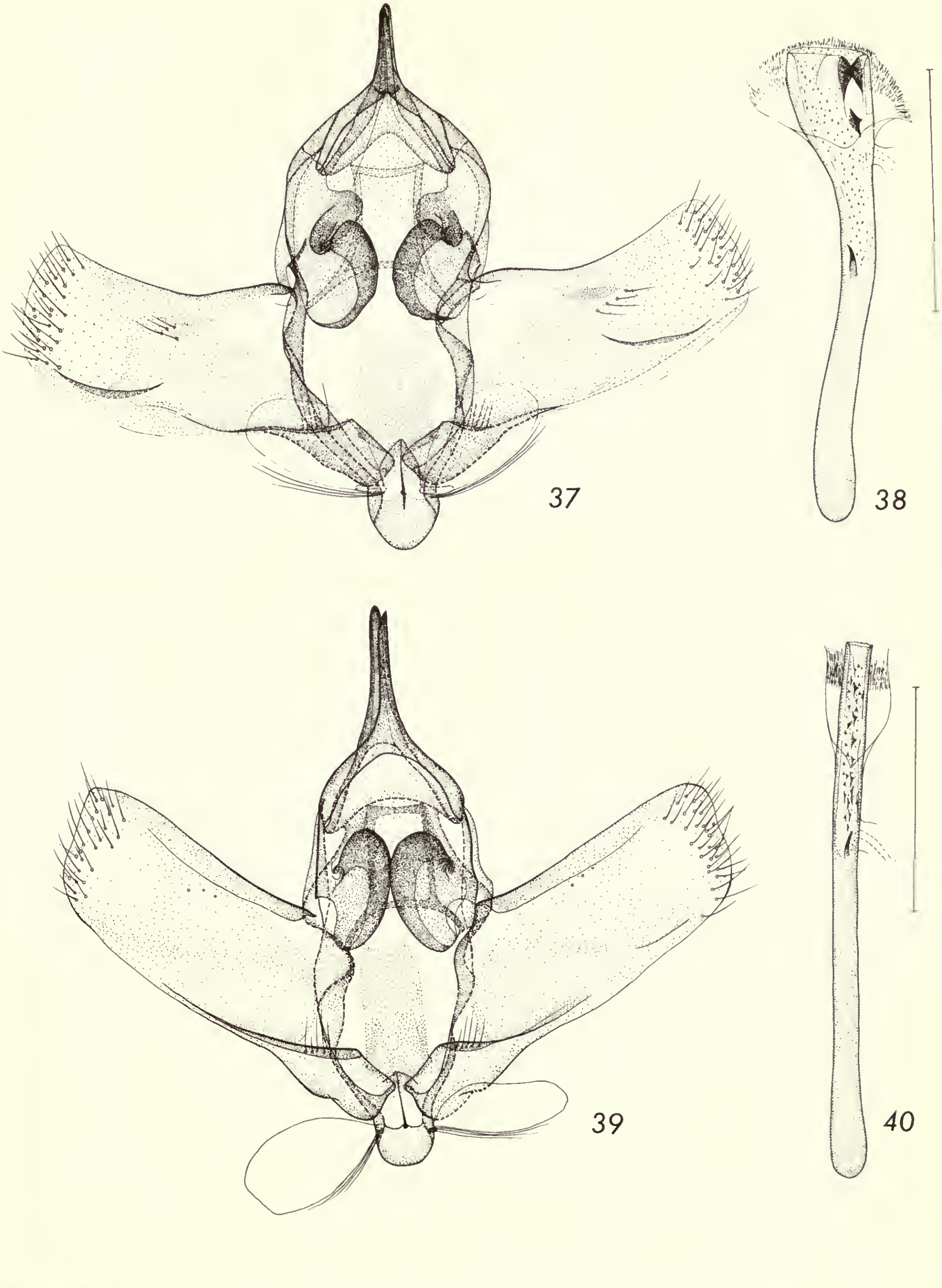


32

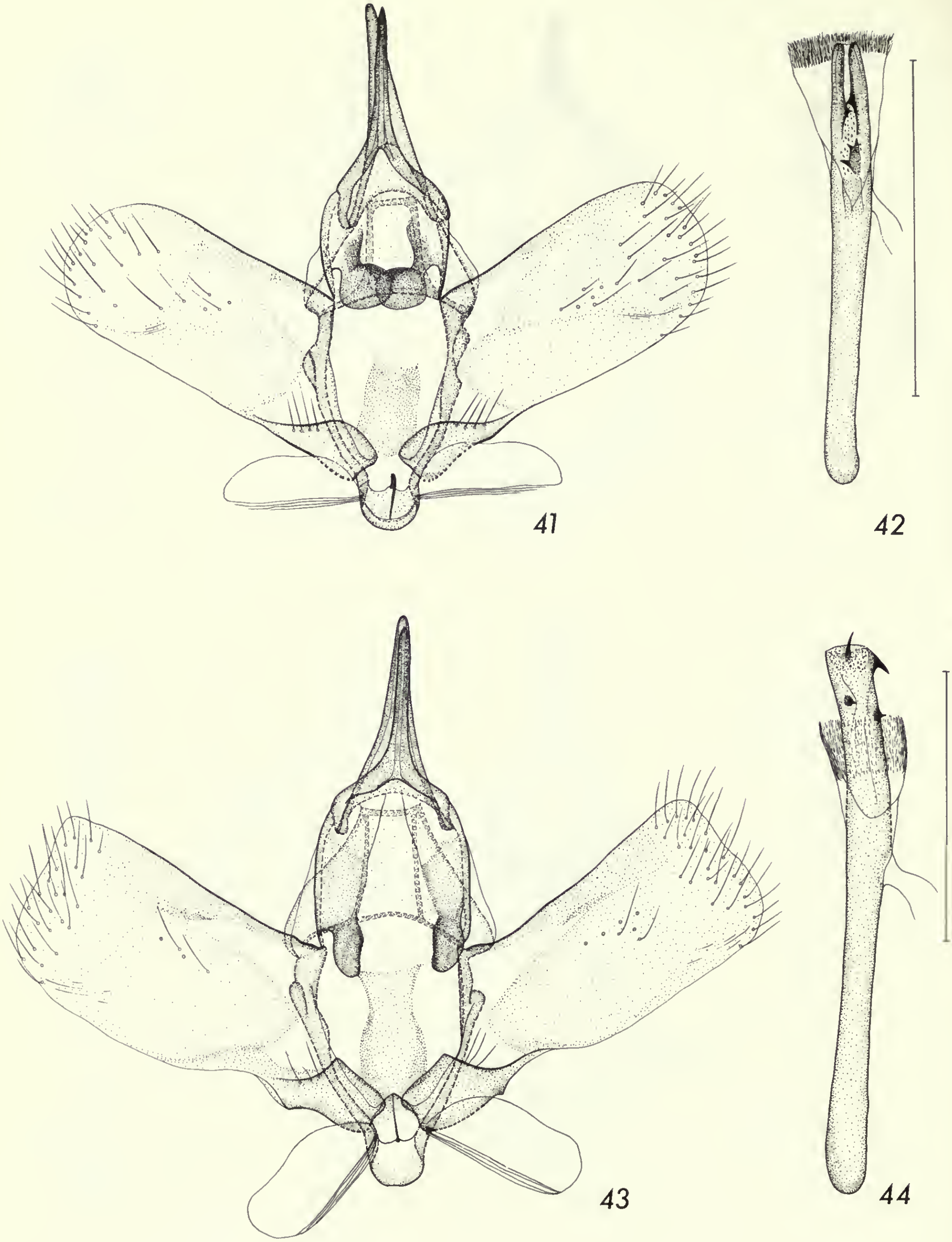
Figs 29–32 Male genitalia. 29, 30, *Scirpophaga praelata* (Scopoli). 31, 32, *S. xanthopygata* Schawerda.



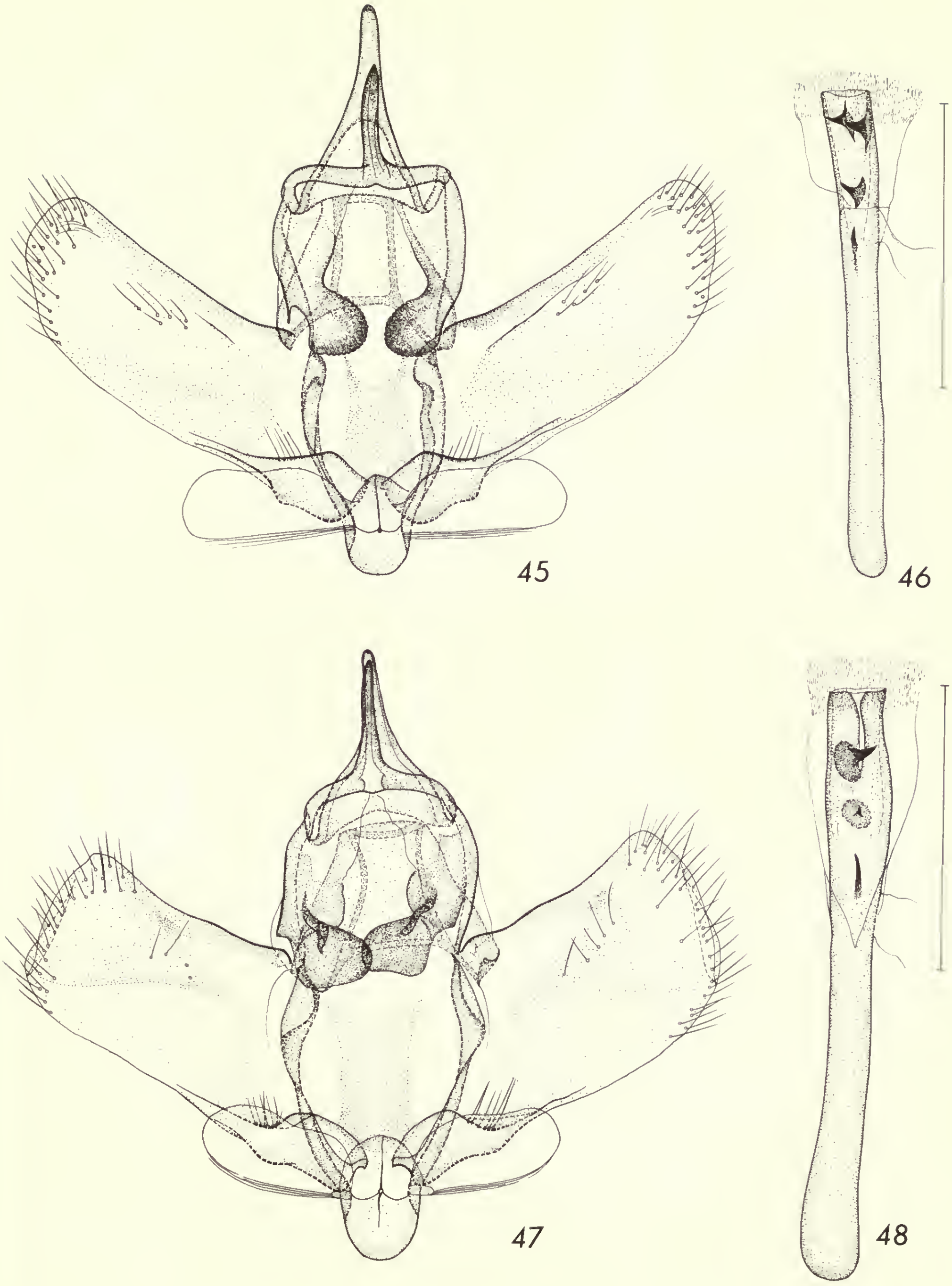
Figs 33–36 Male genitalia. 33, 34, *Scirpophaga nivella* (Fabricius). 35, 36, *S. phaedima* Common.



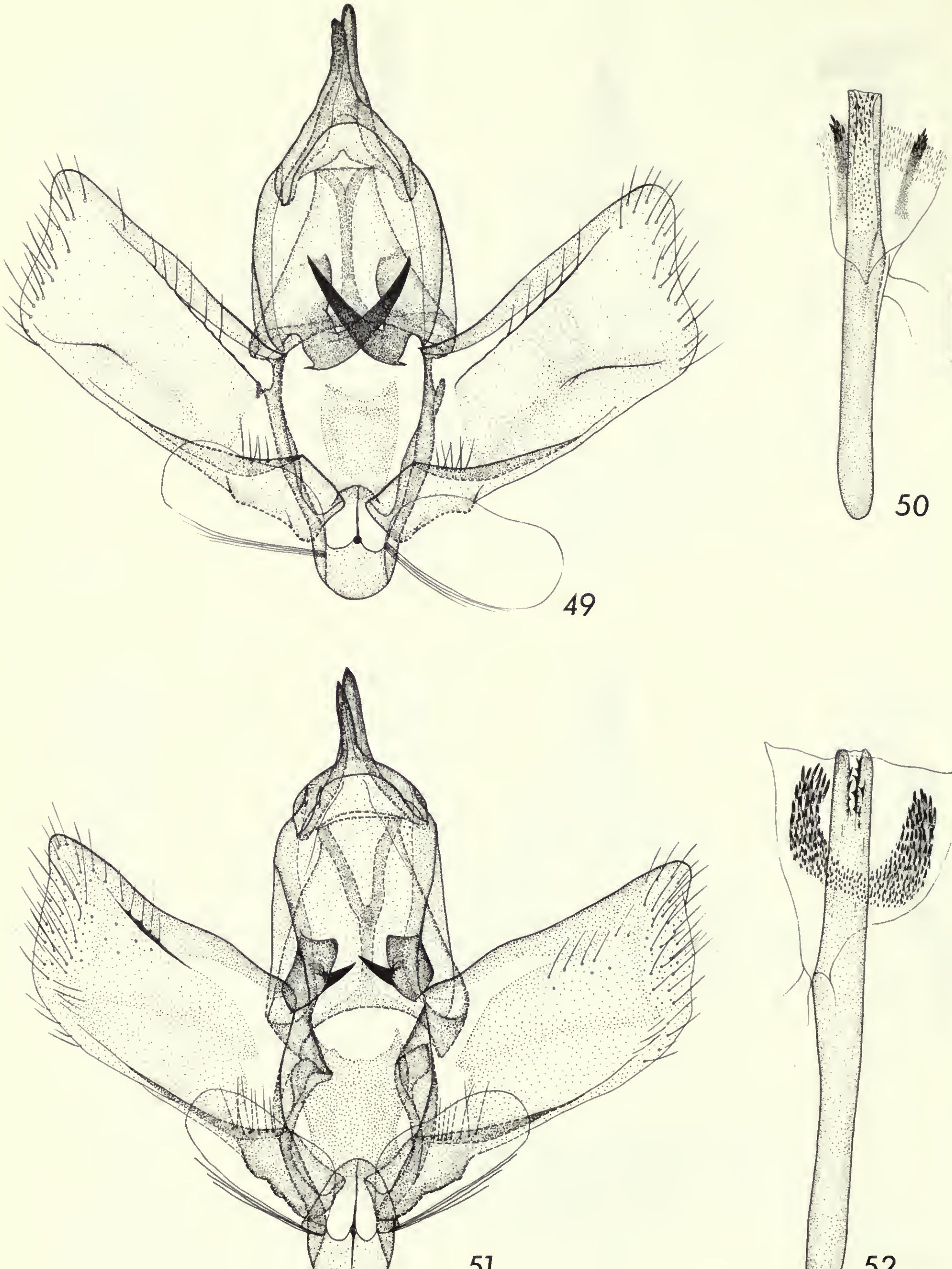
Figs 37–40 Male genitalia. 37, 38, *Scirpophaga parvalis* (Wileman). 39, 40, *S. melanoclista* Meyrick.



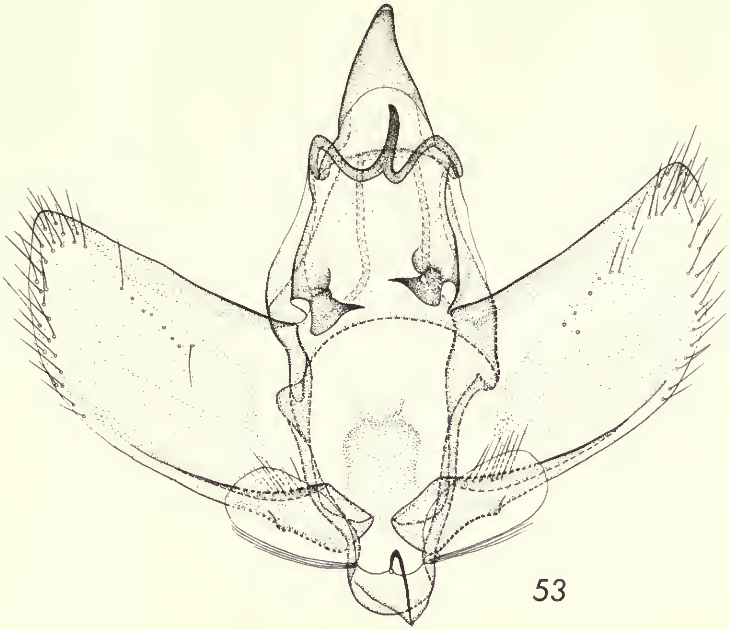
Figs 41–44 Male genitalia. 41, 42, *Scirpophaga gilviberbis* Zeller. 43, 44, *S. percna* Common.



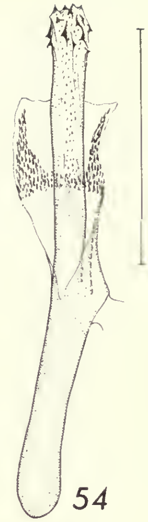
Figs 45–48 Male genitalia. 45, 46, *Scirpophaga imparella* (Meyrick). 47, 48, *S. xantharrenes* Common.



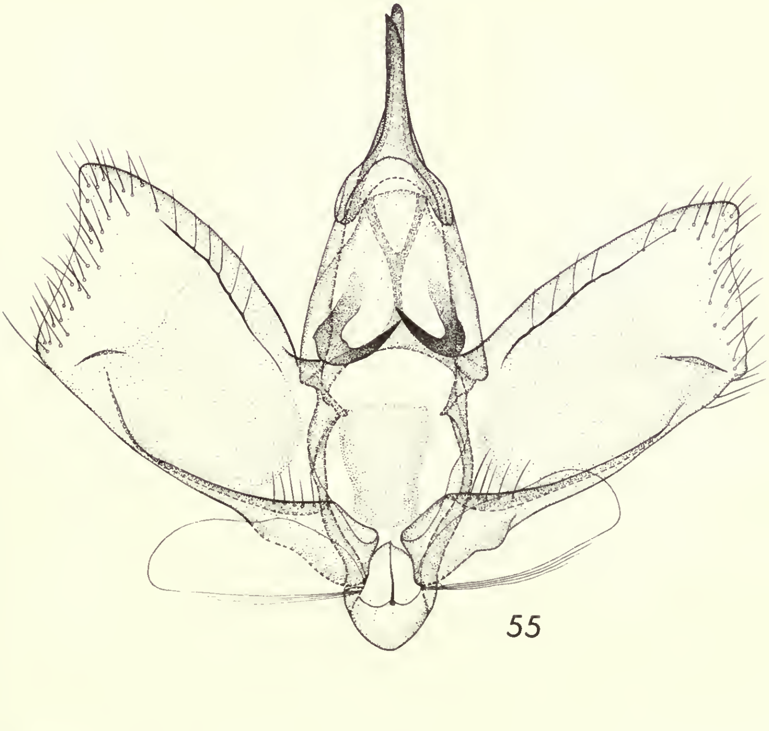
Figs 49–52 Male genitalia. 49, 50, *Scirpophaga excerptalis* (Walker). 51, 52, *S. magnella* de Joannis.



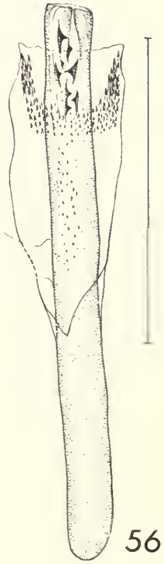
53



54

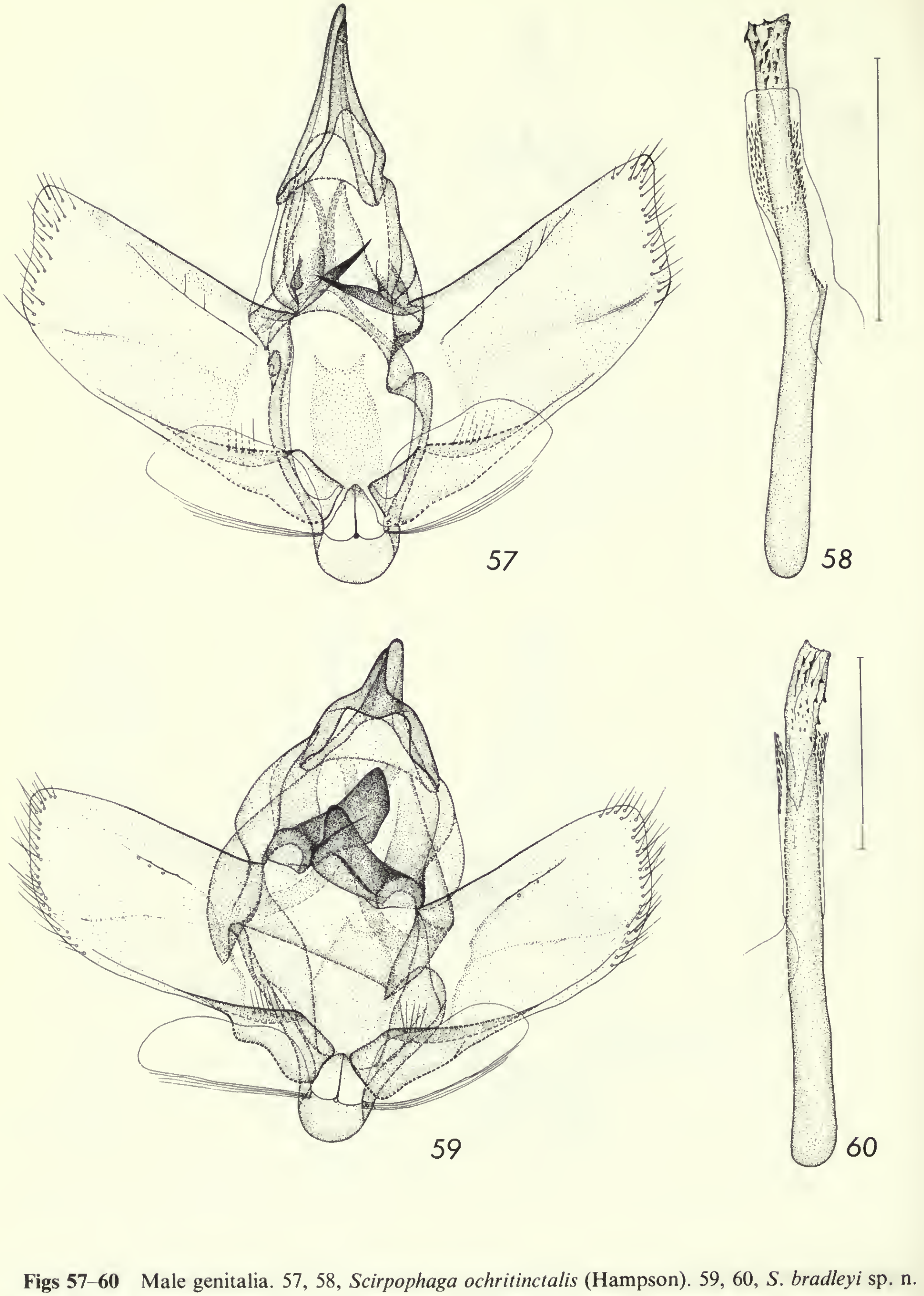


55

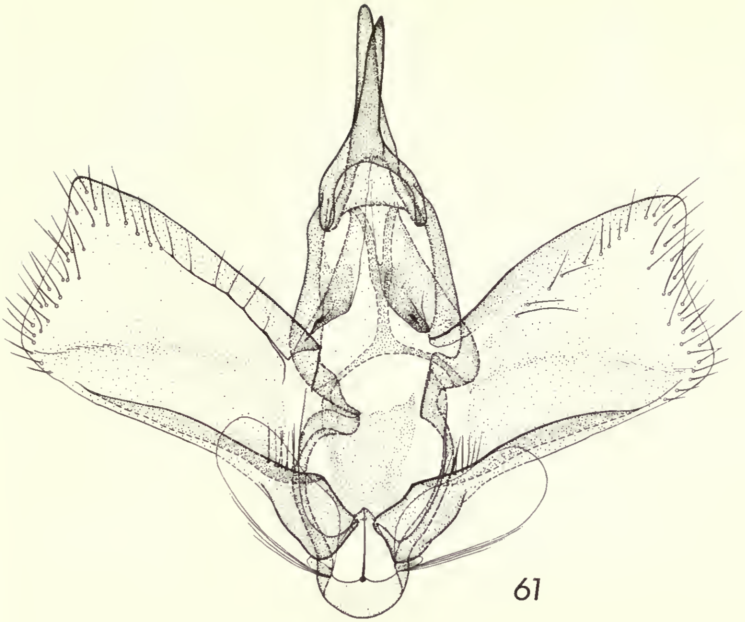


56

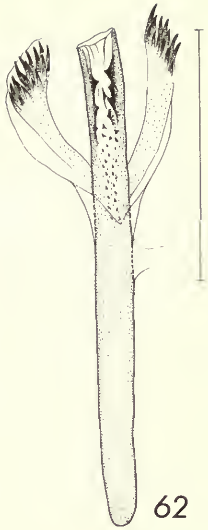
Figs 53–56 Male genitalia. 53, 54, *Scirpophaga tongyaii* sp. n. 55, 56, *S. brunnealis* (Hampson).



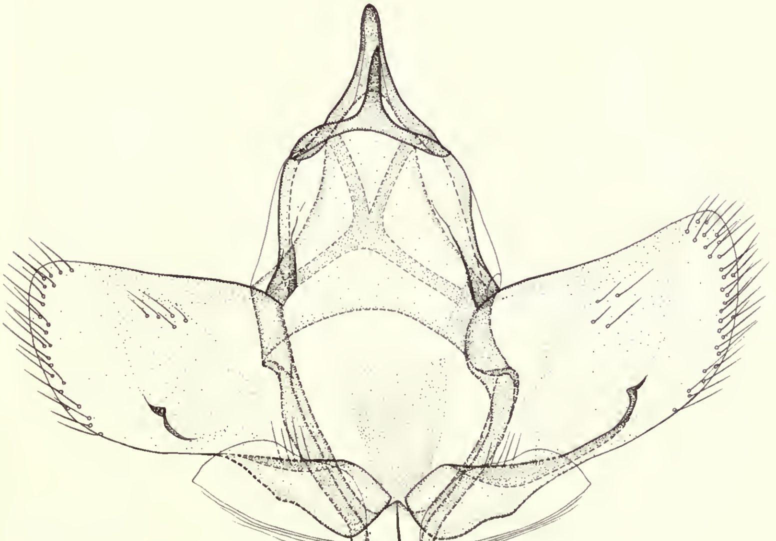
Figs 57–60 Male genitalia. 57, 58, *Scirpophaga ochritinctalis* (Hampson). 59, 60, *S. bradleyi* sp. n.



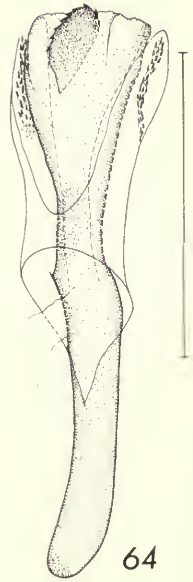
61



62

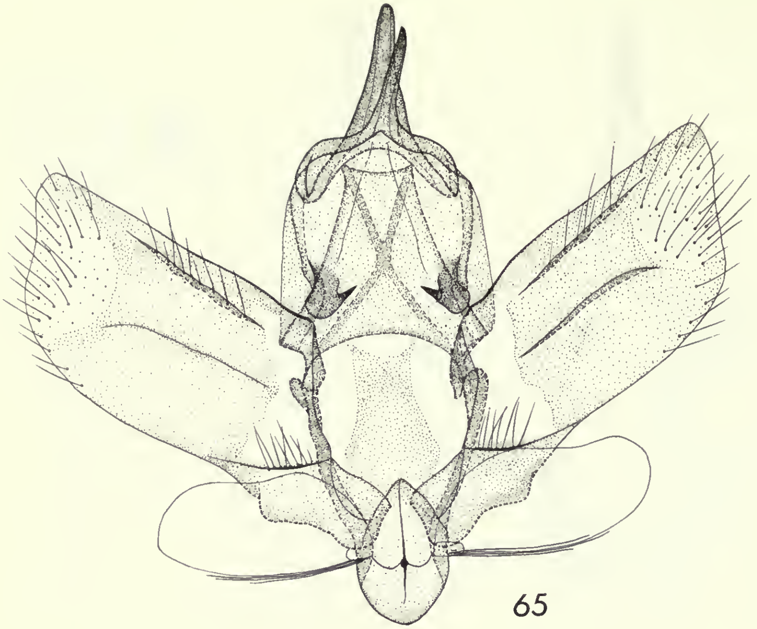


63

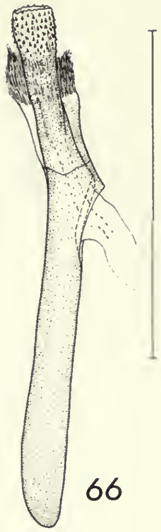


64

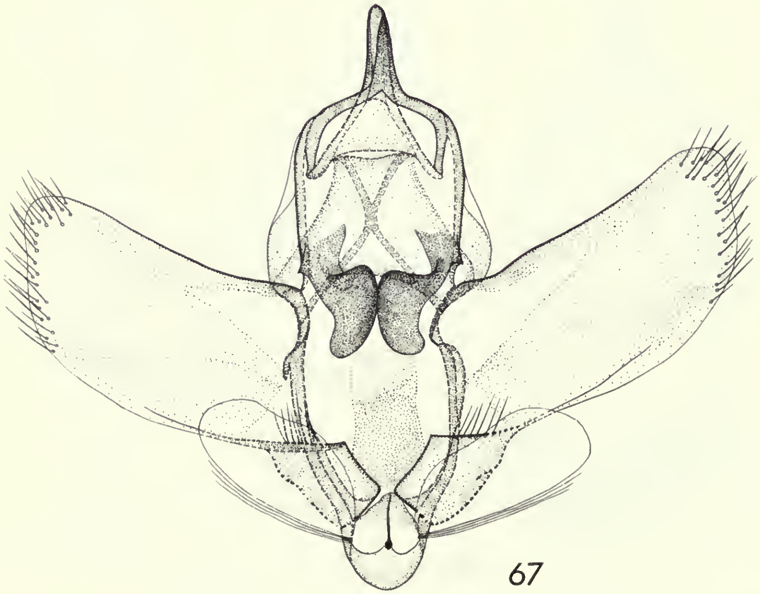
Figs 61–64 Male genitalia. 61, 62, *Scirpophaga khasis* sp. n. 63, 64, *S. flavidorsalis* (Hampson).



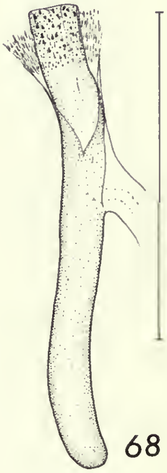
65



66

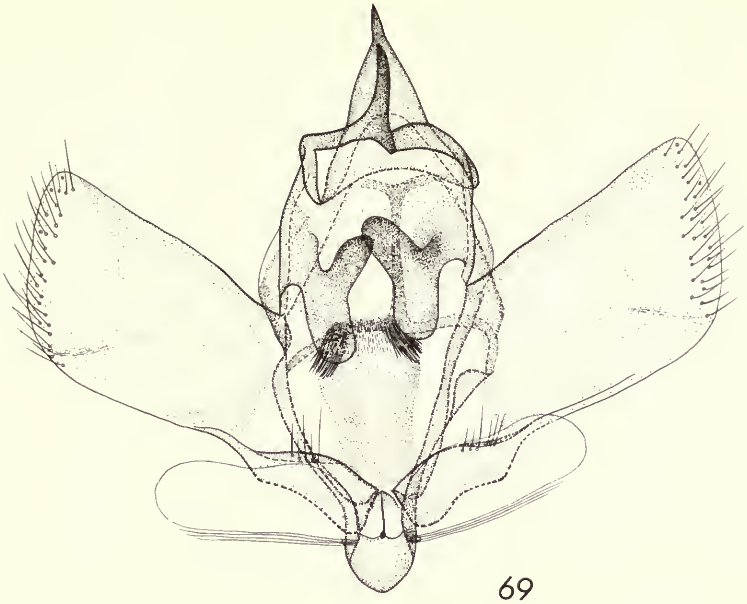


67

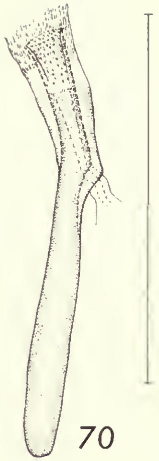


68

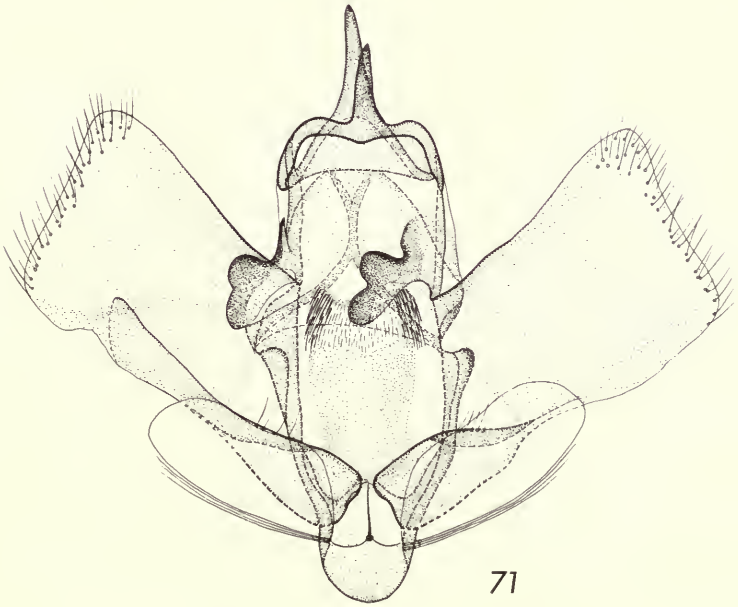
Figs 65–68 Male genitalia. 65, 66, *Scirpophaga xanthogastrella* (Walker). 67, 68, *S. gotoi* sp. n.



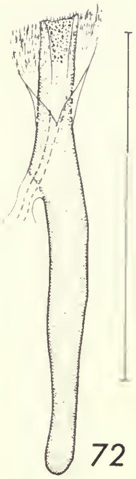
69



70

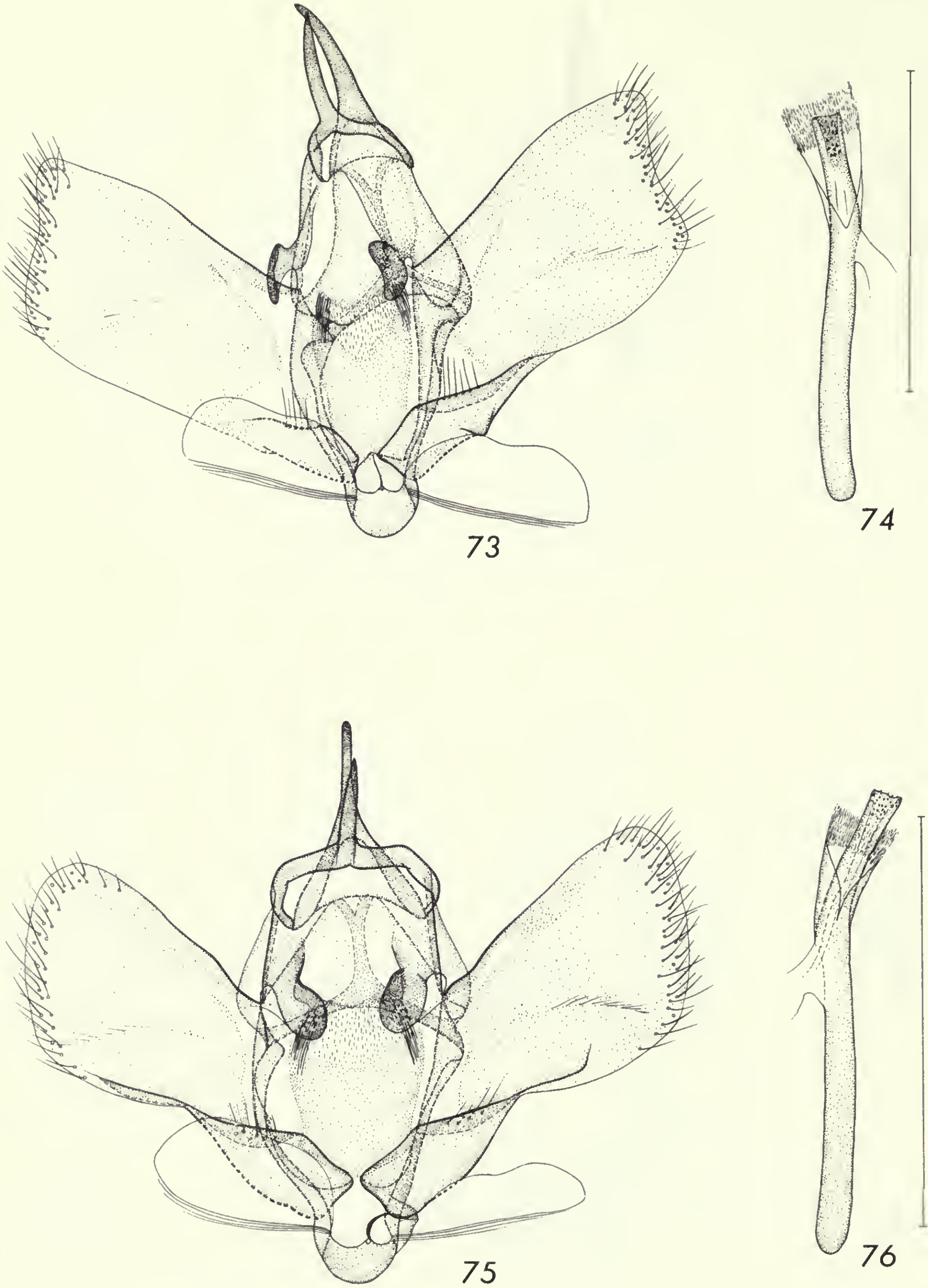


71

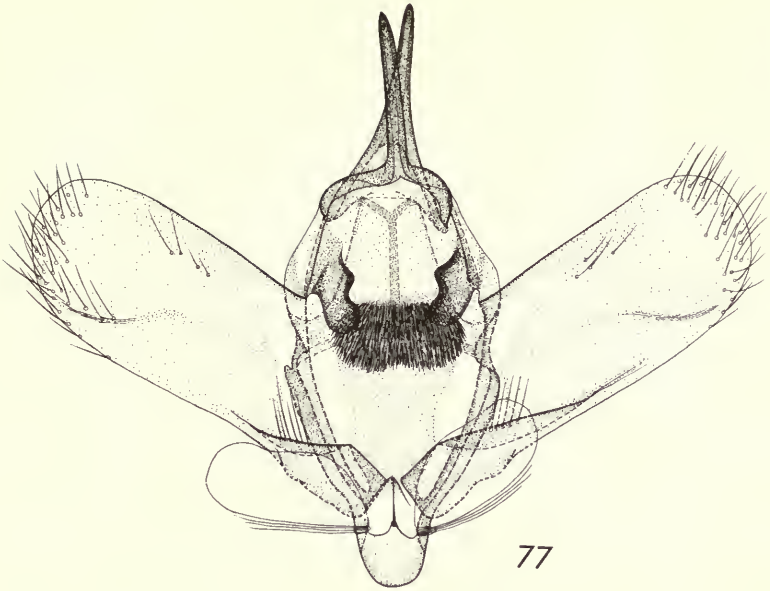


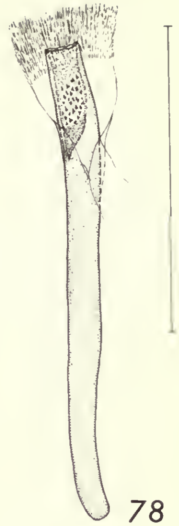
72

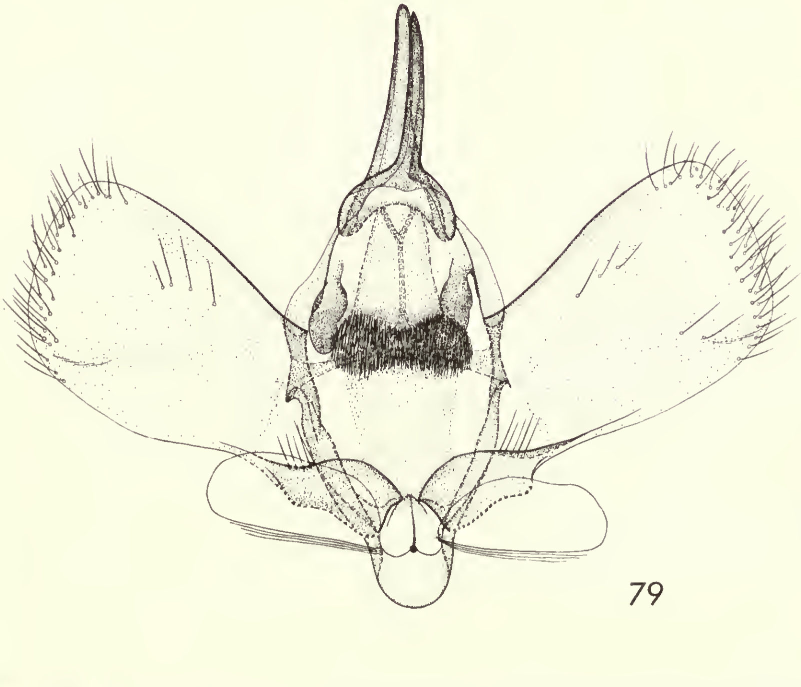
Figs 69–72 Male genitalia. 69, 70, *Scirpophaga occidentella* (Walker). 71, 72, *S. fusciflua* Hampson.

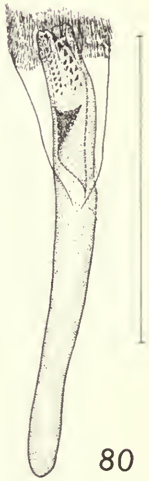


Figs 73–76 Male genitalia. 73, 74, *Scirpophaga ochroleuca* Meyrick. 75, 76, *S. virginia* Schultze.

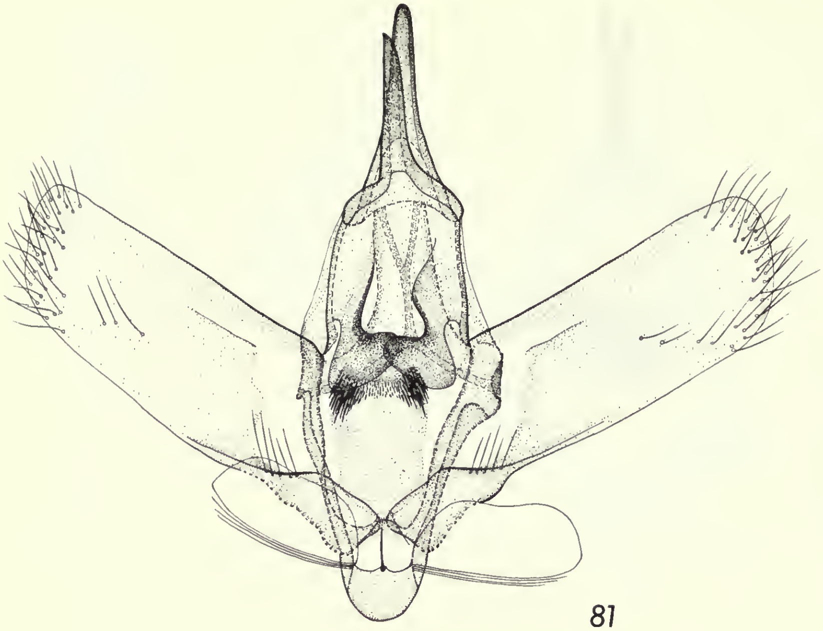

77


78

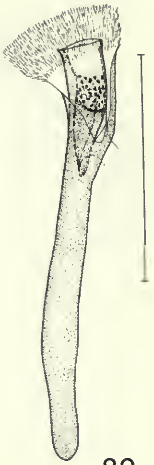

79


80

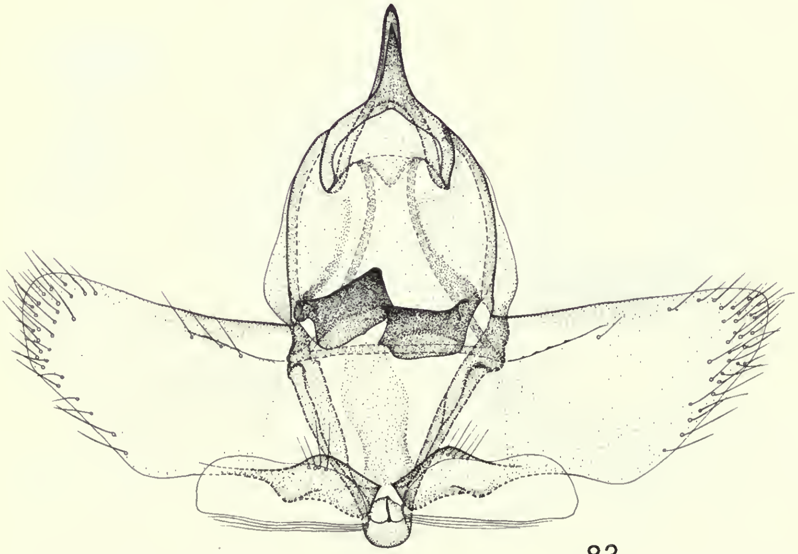
Figs 77–80 Male genitalia. 77, 78, *Scirpophaga subumbrosa* Meyrick. 79, 80, *S. marginepunctella* (de Joannis).



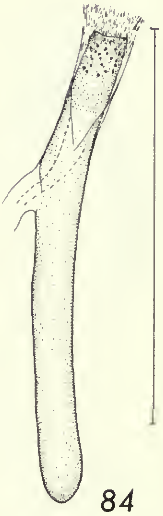
81



82

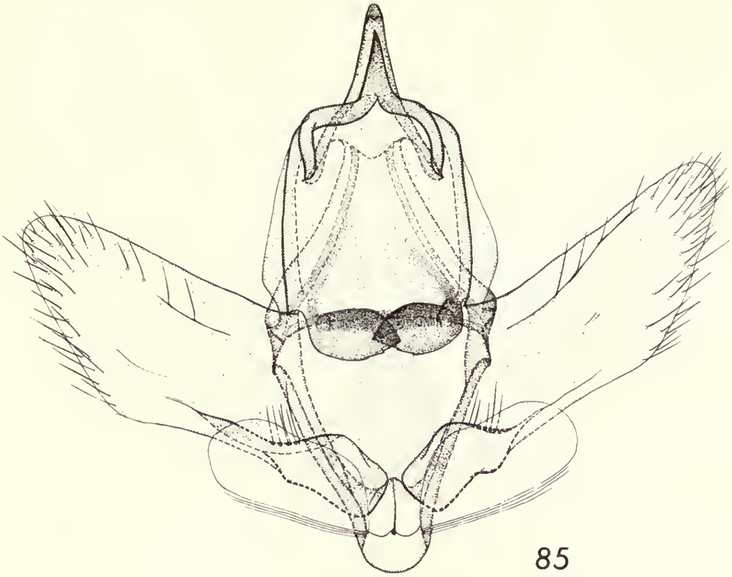


83

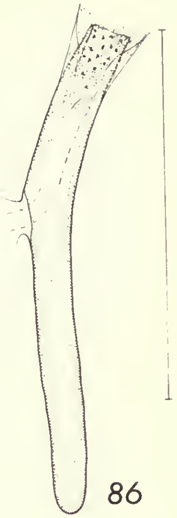


84

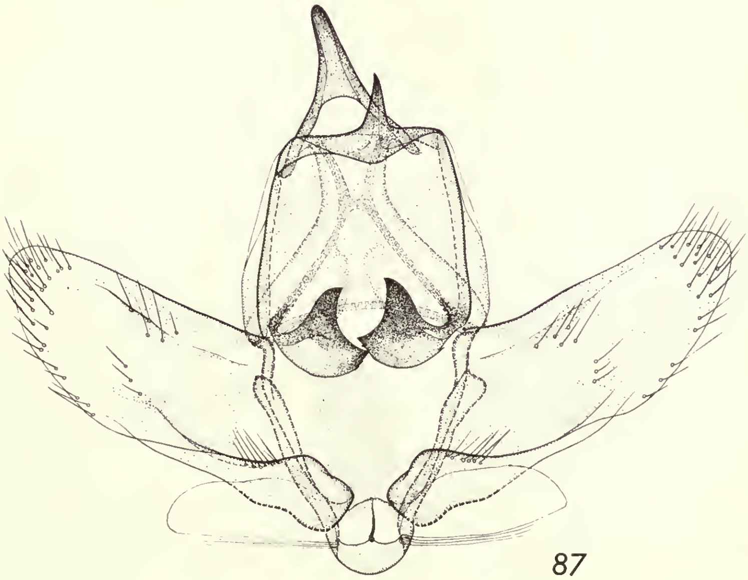
Figs 81–84 Male genitalia. 81, 82, *Scirpophaga serena* (Meyrick). 83, 84, *S. lineata* (Butler).



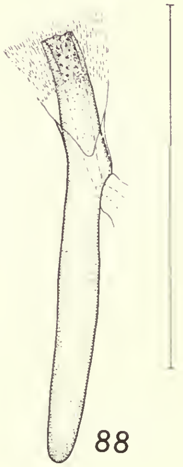
85



86

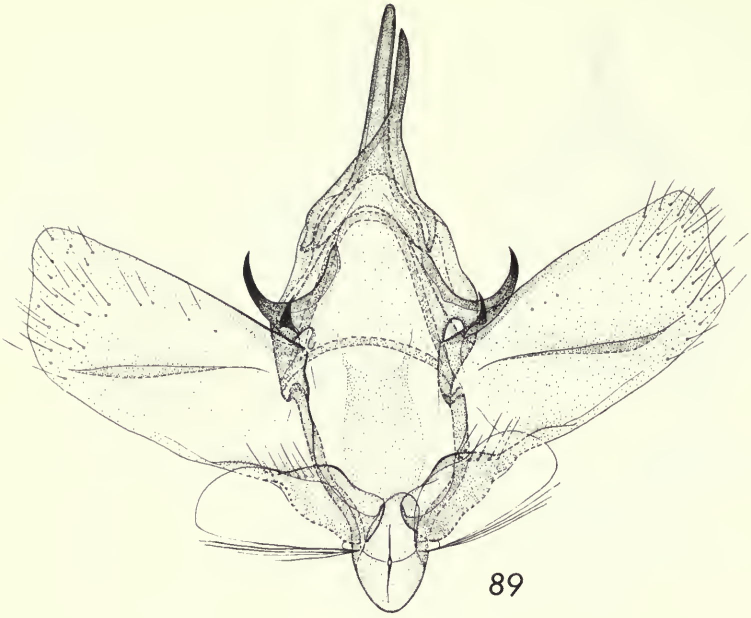


87

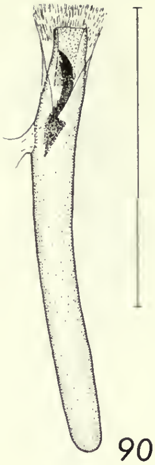


88

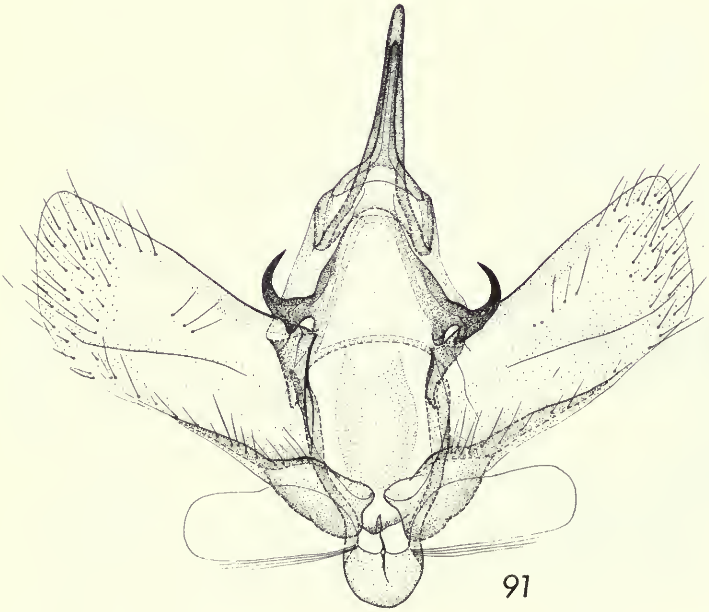
Figs 85–88 Male genitalia. 85, 86, *Scirpophaga aurivena* (Hampson). 87, 88, *S. auristrigella* (Hampson).



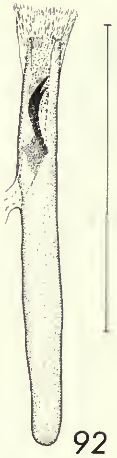
89



90

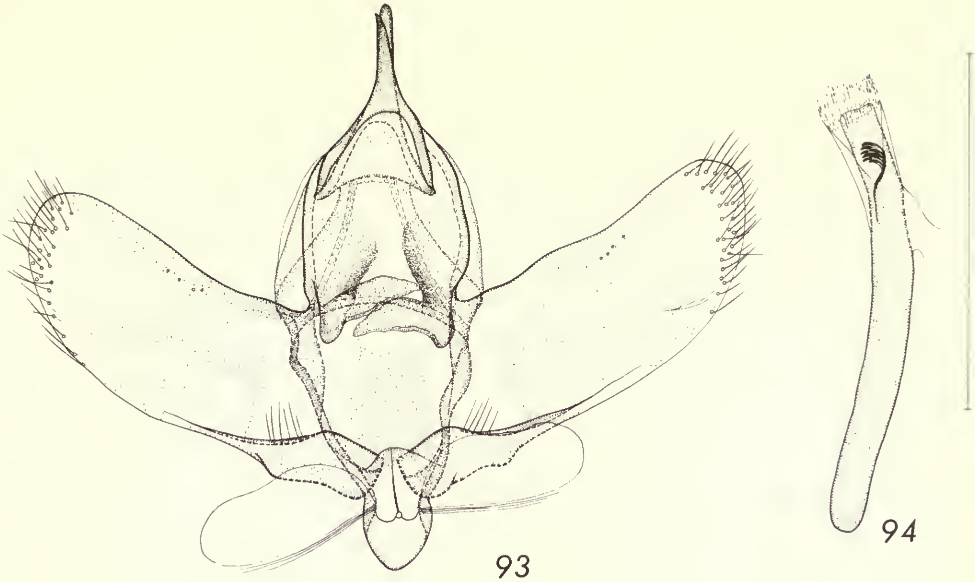


91

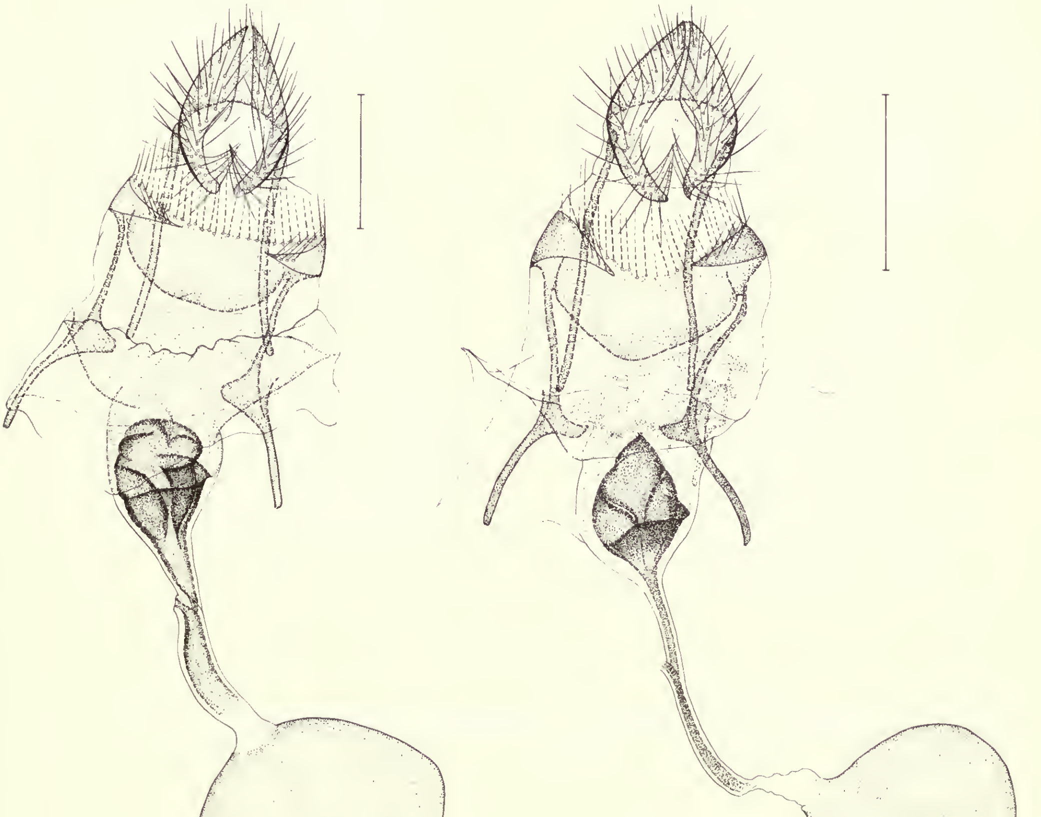


92

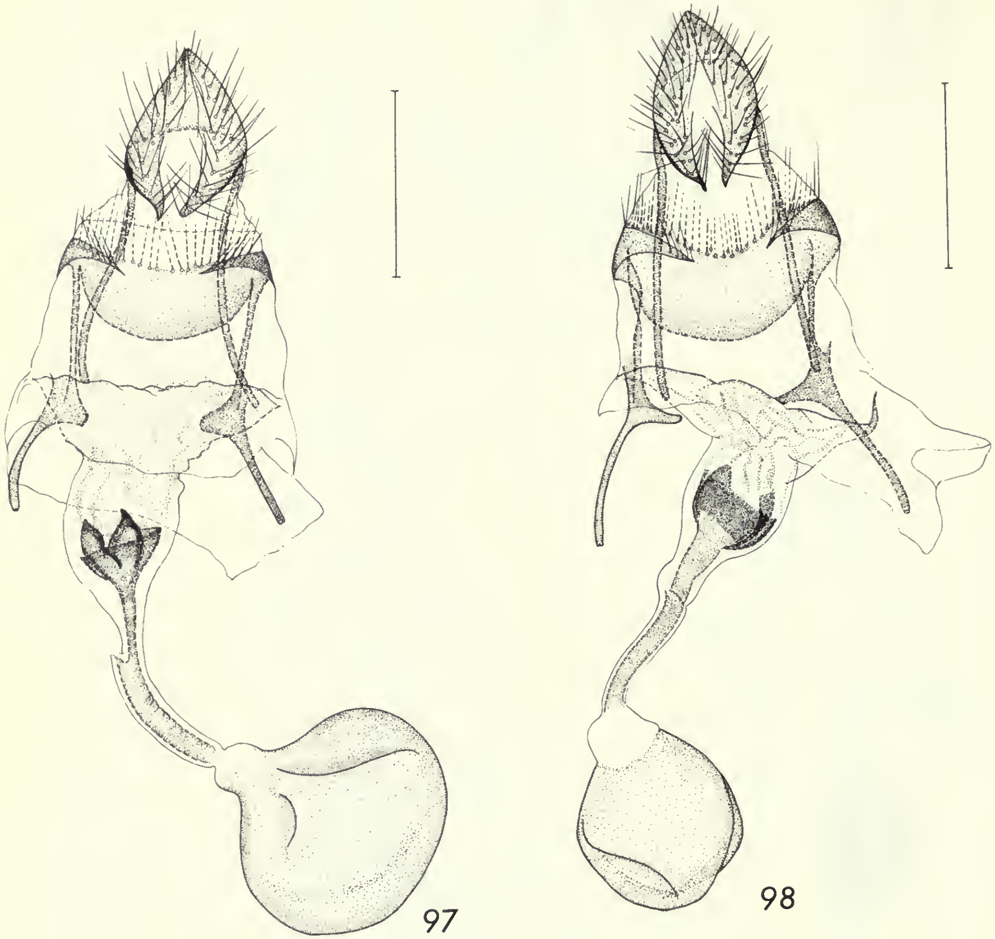
Figs 89–92 Male genitalia. 89, 90, *Scirpophaga incertulas* (Walker). 91, 92, *S. innotata* (Walker).



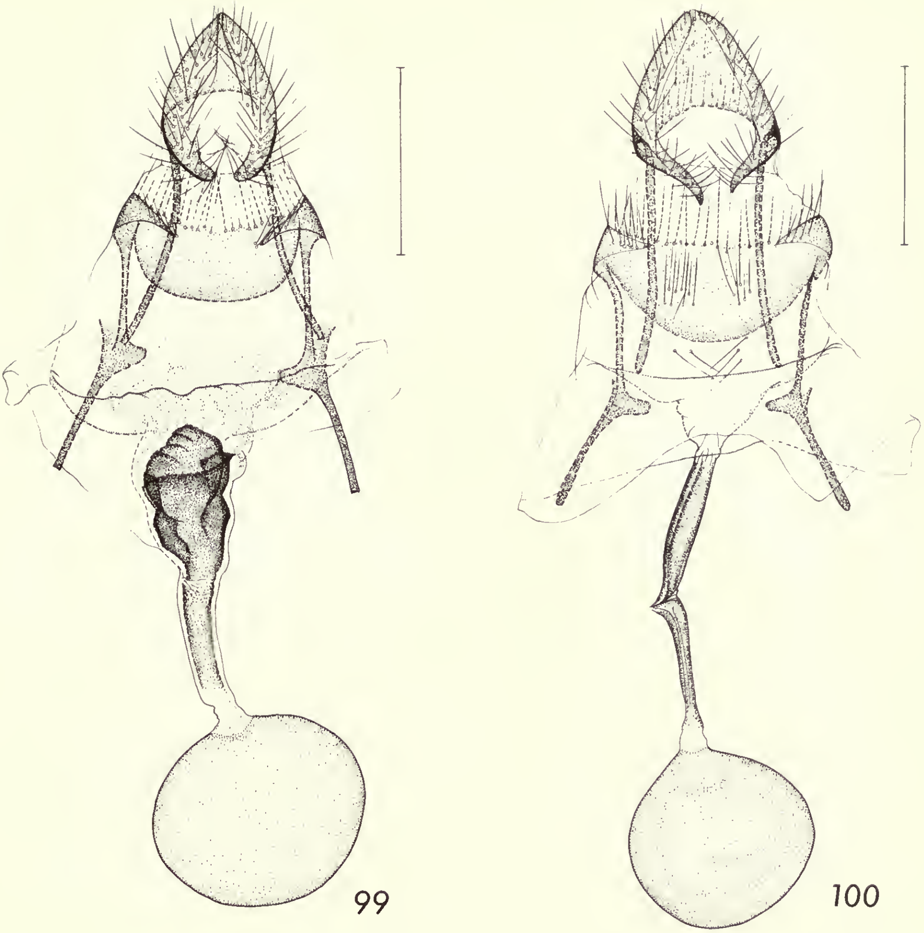
Figs 93–94 Male genitalia of *Scirpophaga whalleyi* sp. n.



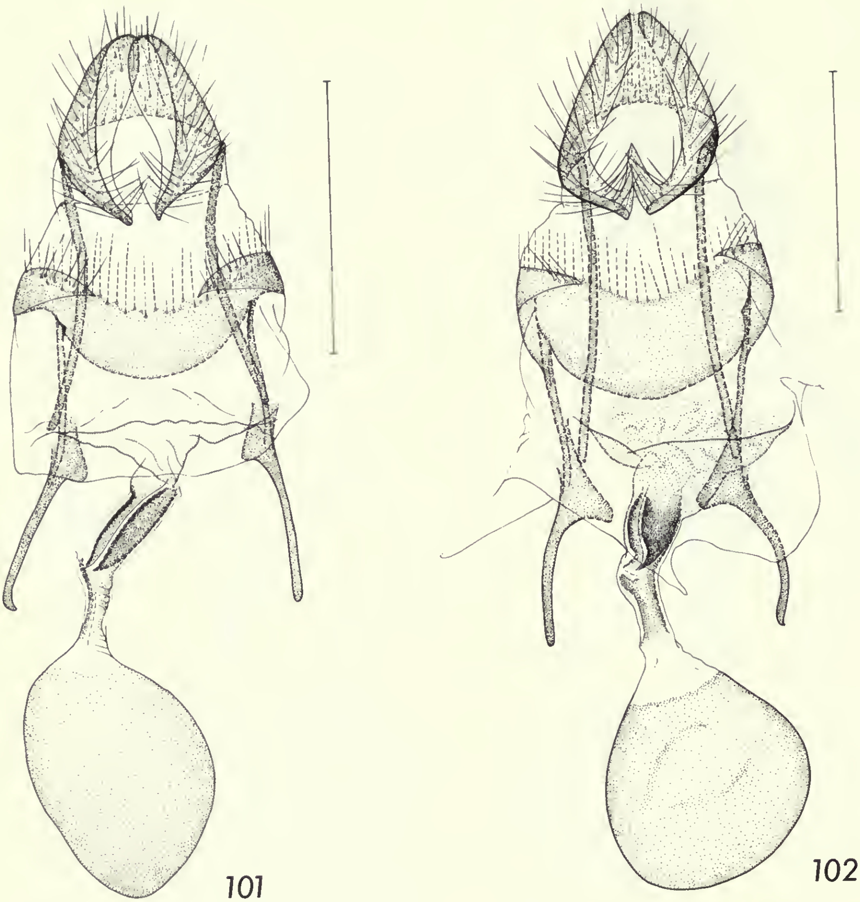
Figs 95, 96 Female genitalia. 95, *Scirpophaga praelata* (Scopoli). 96, *S. xanthopygata* Schawerda.



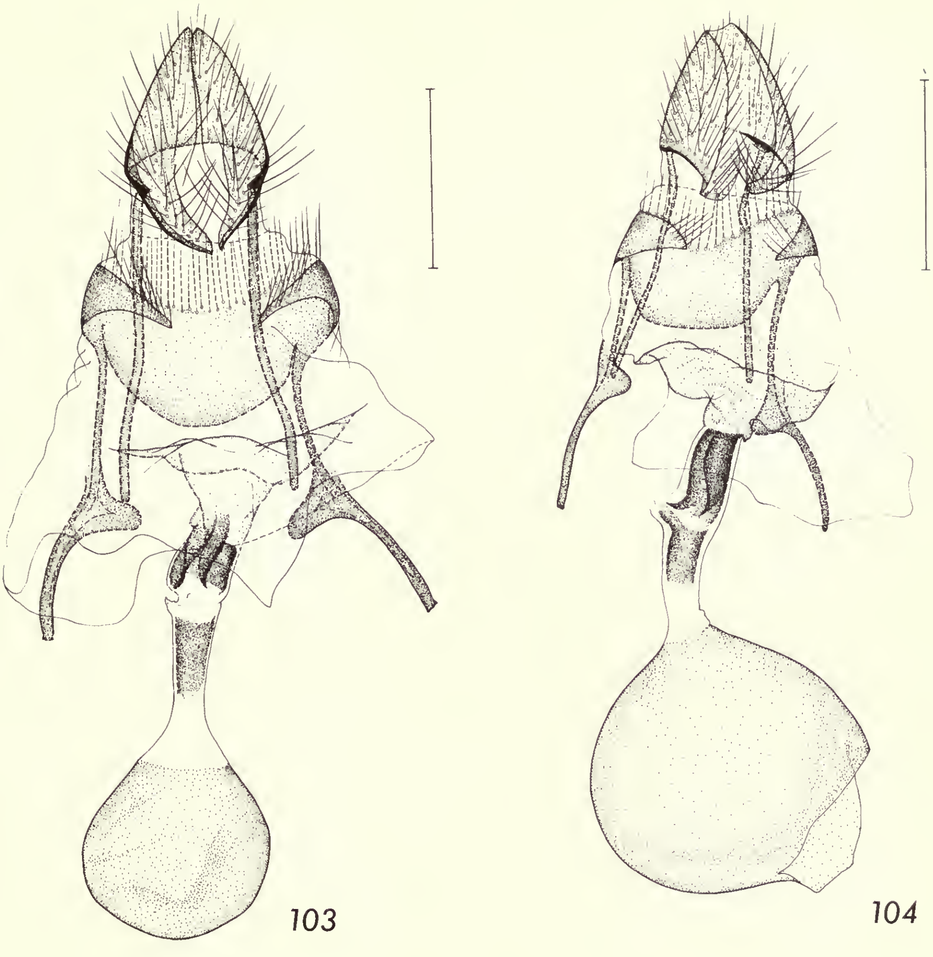
Figs 97, 98 Female genitalia of *Scirpophaga nivella* (Fabricius).



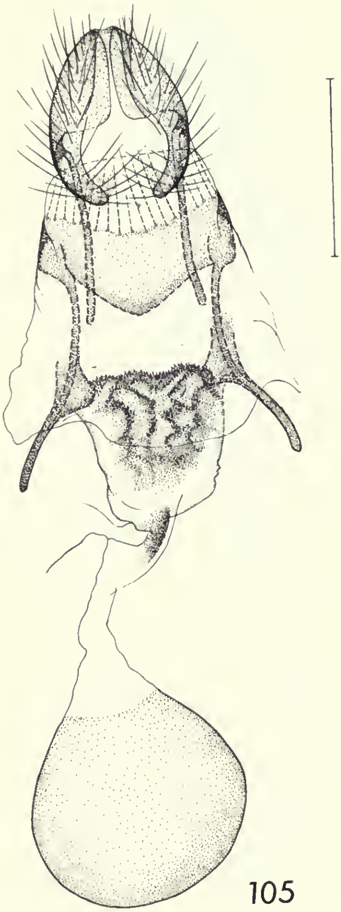
Figs 99, 100 Female genitalia. 99, *Scirpophaga parvalis* (Wileman). 100, *S. melanoclista* Meyrick.



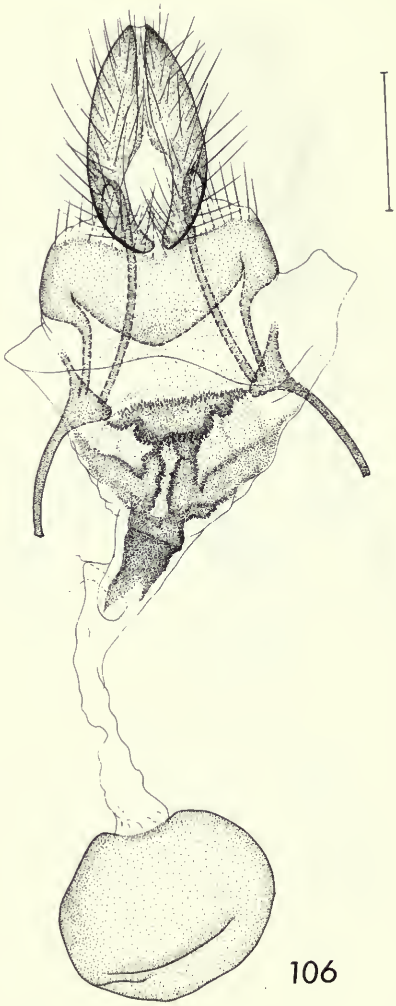
Figs 101, 102 Female genitalia. 101, *Scirpophaga gilviberbis* Zeller. 102, *S. percna* Common.



Figs 103, 104 Female genitalia. 103, *Scirpophaga imparella* (Meyrick). 104, *S. xantharrenes* Common.

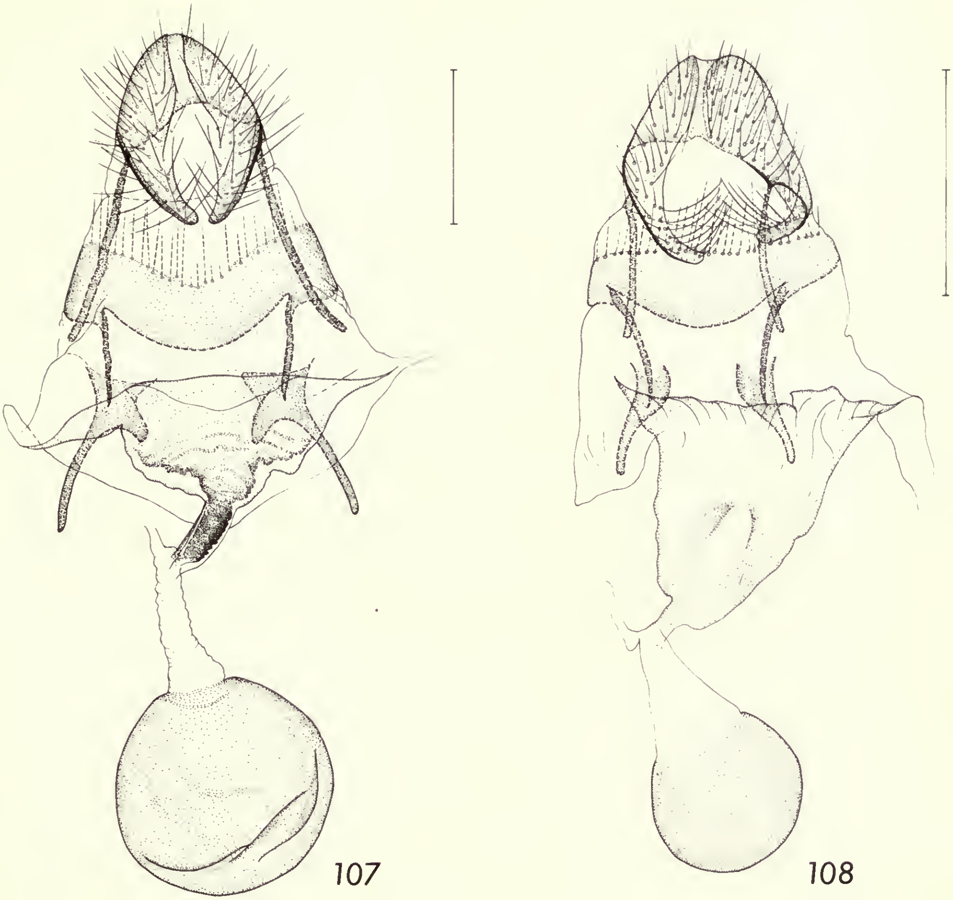


105

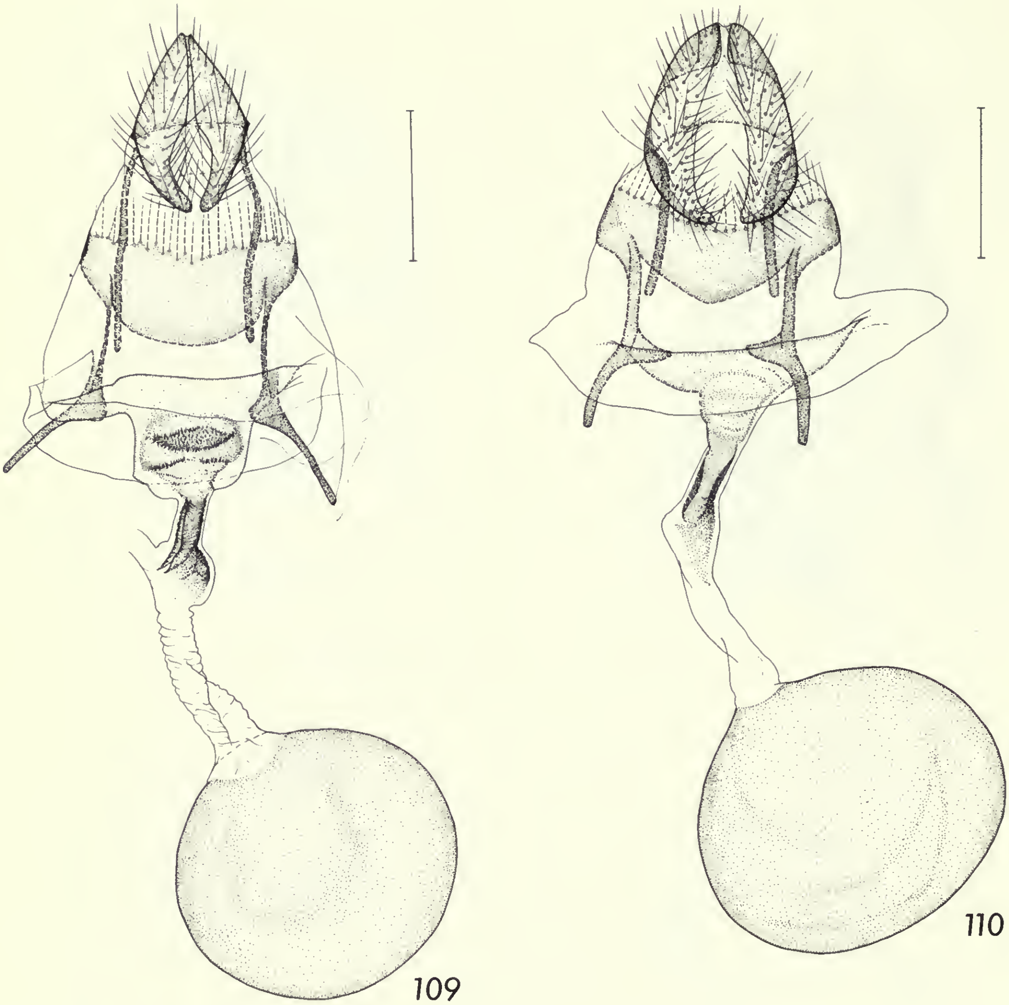


106

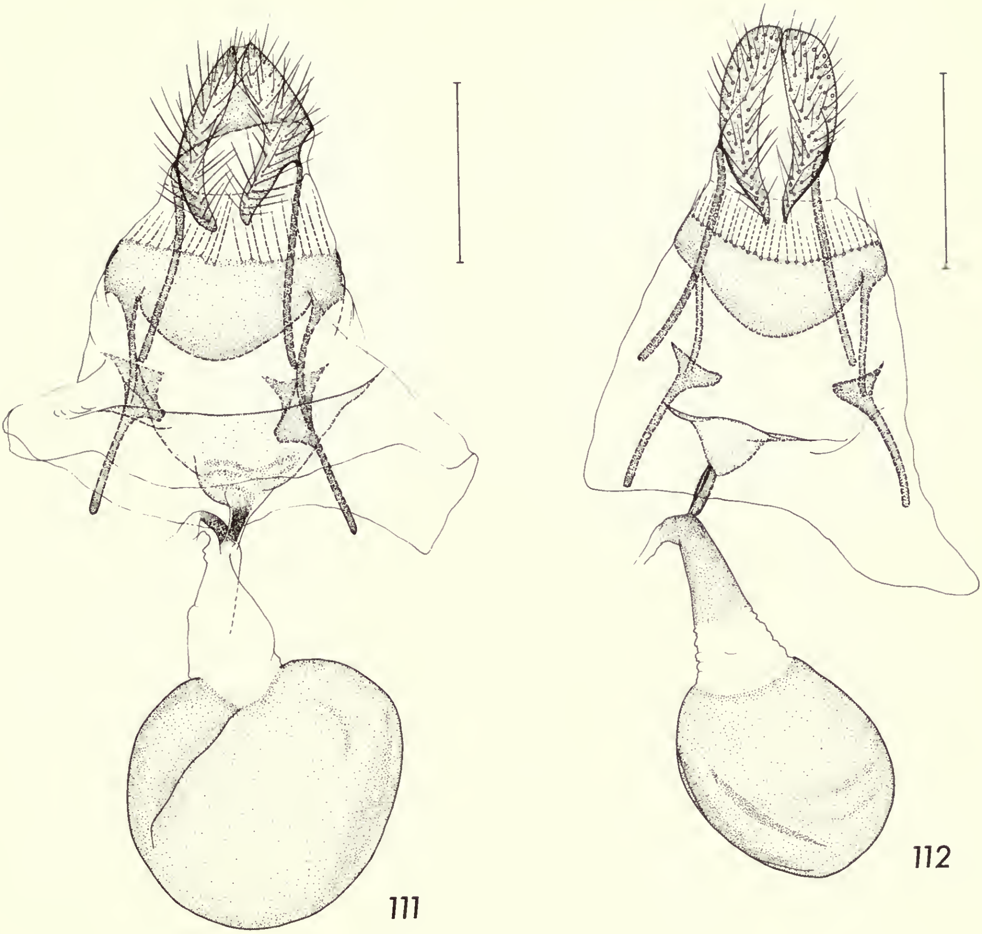
Figs 105, 106 Female genitalia. 105, *Scirpophaga excerptalis* (Walker). 106, *S. magnella* de Joannis.



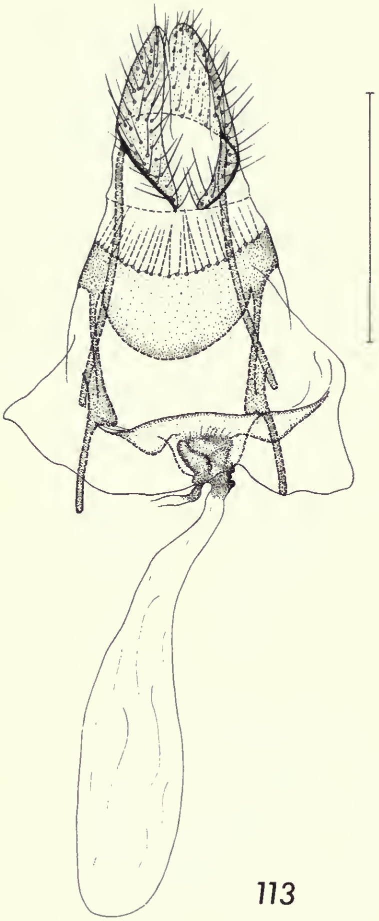
Figs 107, 108 Female genitalia. 107, *Scirpophaga tongyaii* sp. n. 108, *S. melanostigma* (Turner).

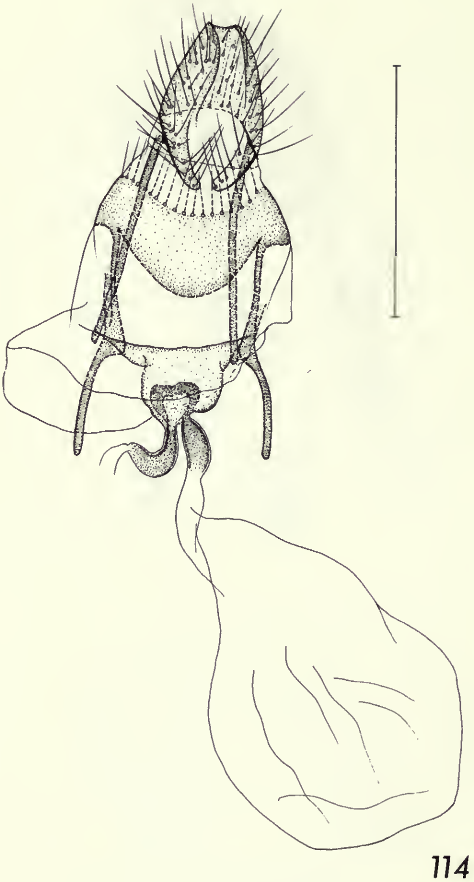


Figs 109, 110 Female genitalia. 109, *Scirpophaga ochritinctalis* (Hampson). 110, *S. bradleyi* sp. n.

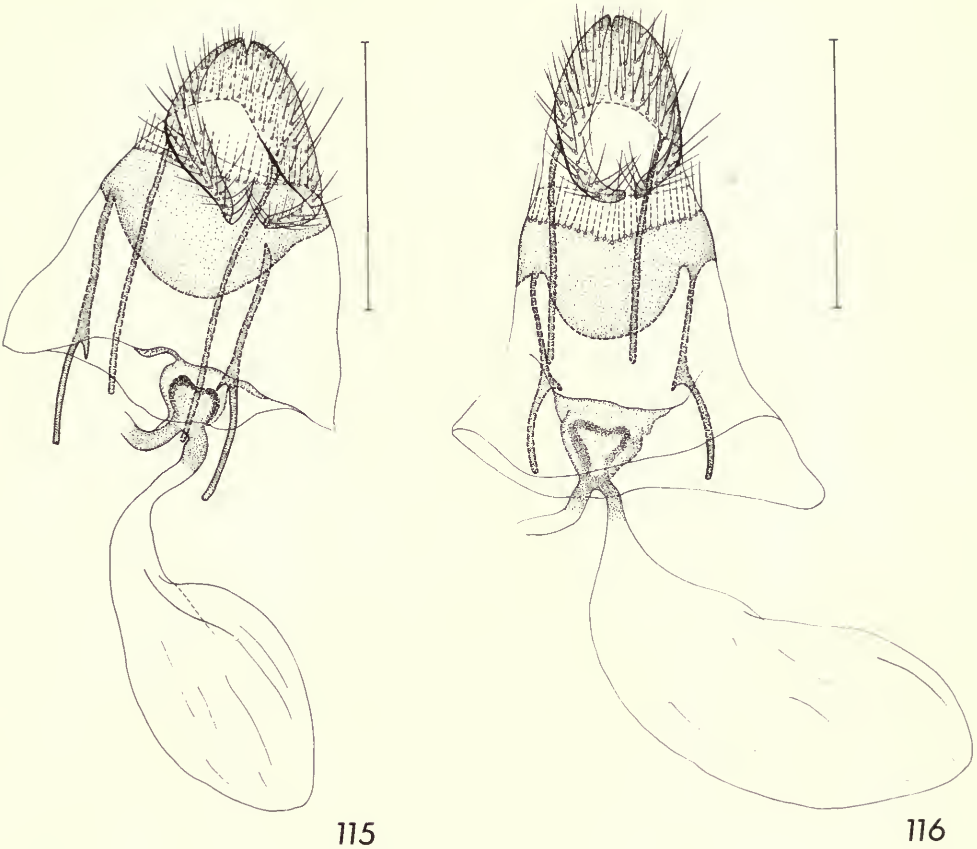


Figs 111, 112 Female genitalia. 111, *Scirpophaga xanthogastrella* (Walker). 112, *S. gotoi* sp. n.

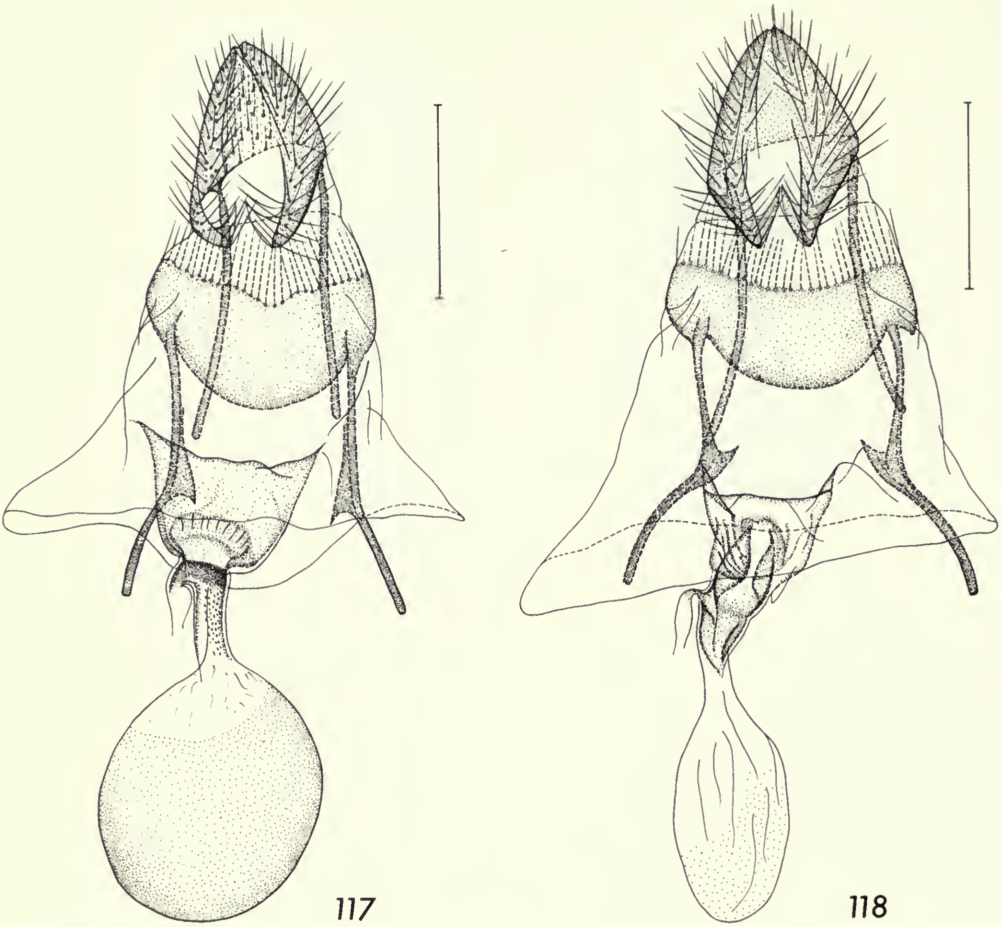




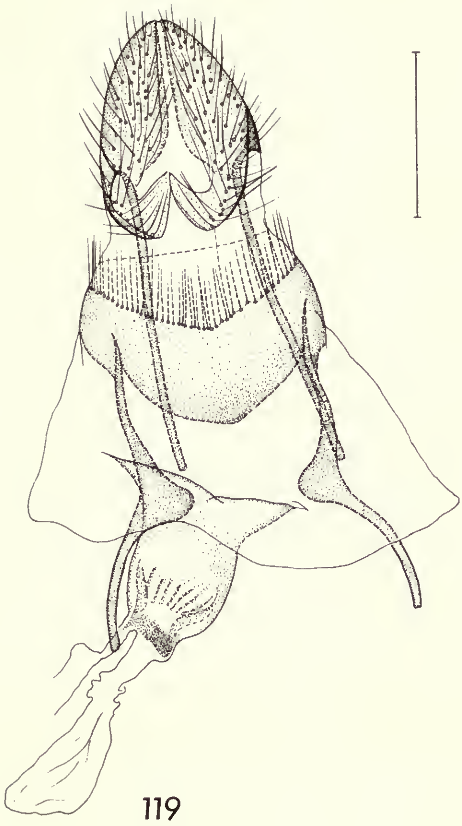
Figs 113, 114 Female genitalia. 113, *Scirpophaga occidentella* (Walker). 114, *S. fusciflua* Hampson.

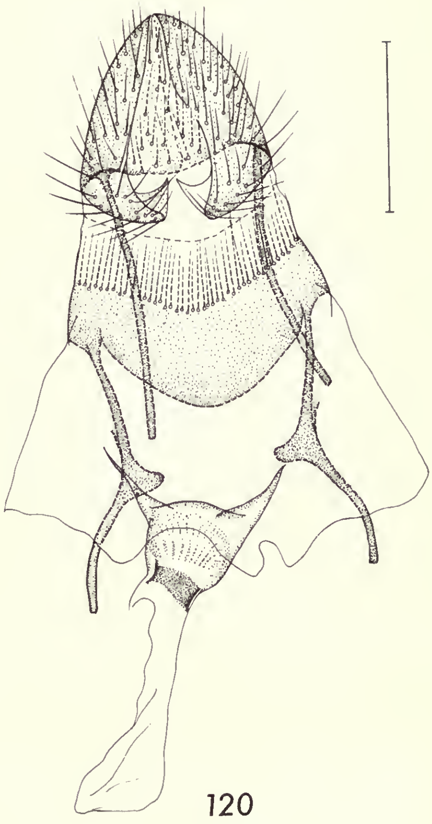


Figs 115, 116 Female genitalia. 115, *Scirpophaga ochroleuca* Meyrick. 116, *S. virginia* Schultze.

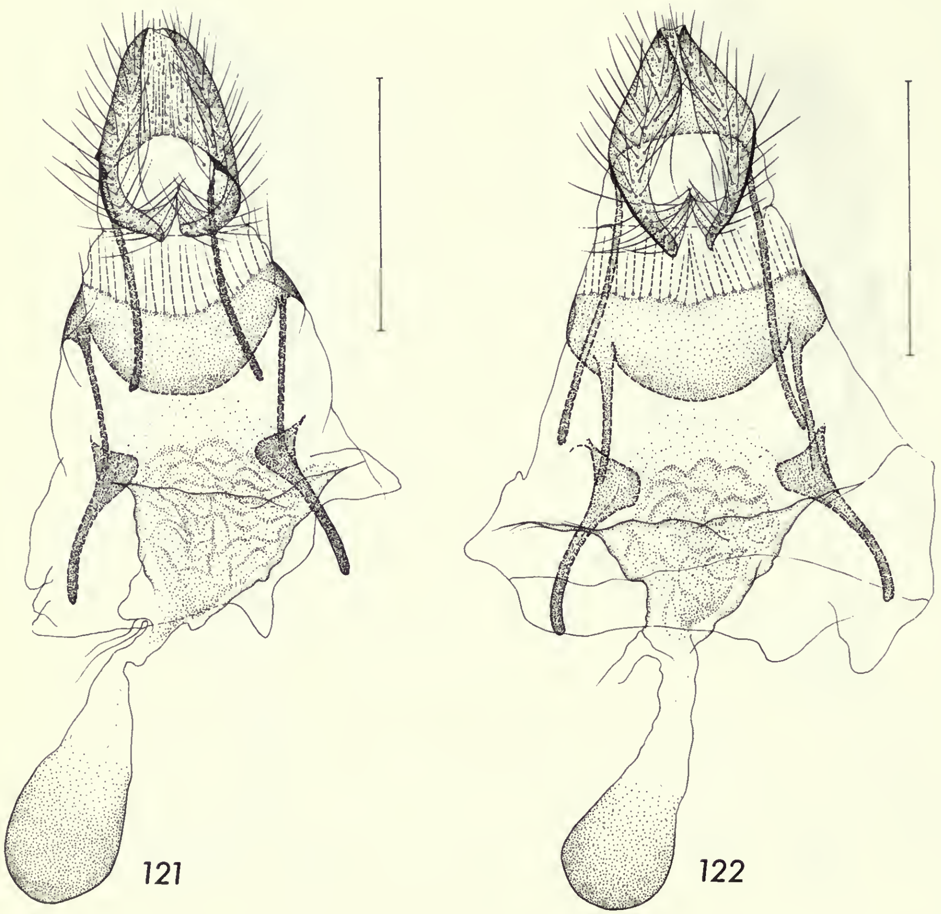


Figs 117, 118 Female genitalia. 117, *Scirpophaga subumbrosa* Meyrick. 118, *S. marginepunctella* (de Joannis).

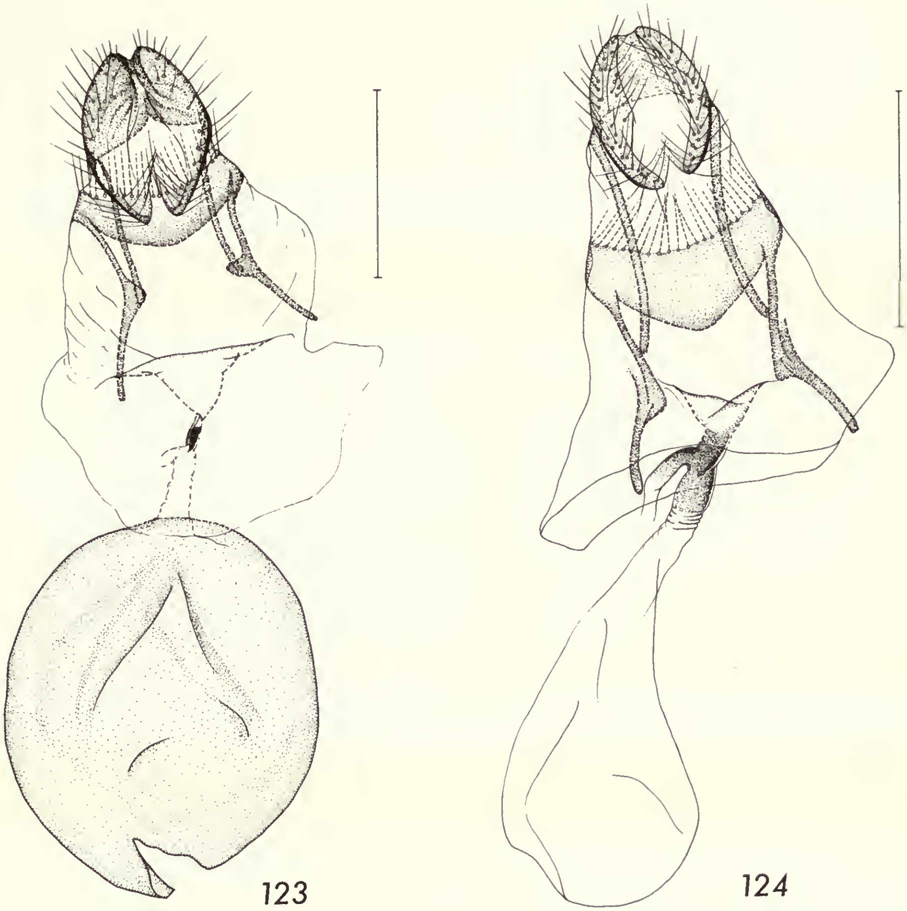

119


120

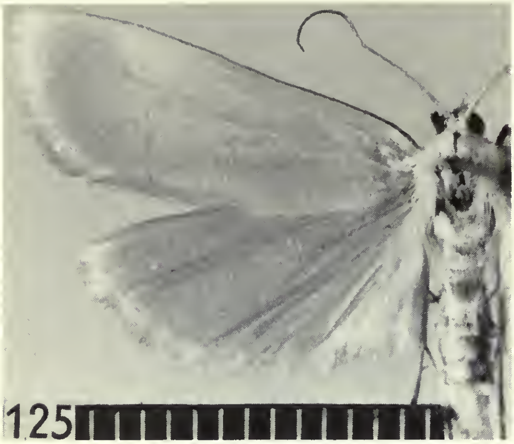
Figs 119, 120 Female genitalia. 119, *Scirpophaga serena* (Meyrick). 120, *S. goliath* Marion & Viette.

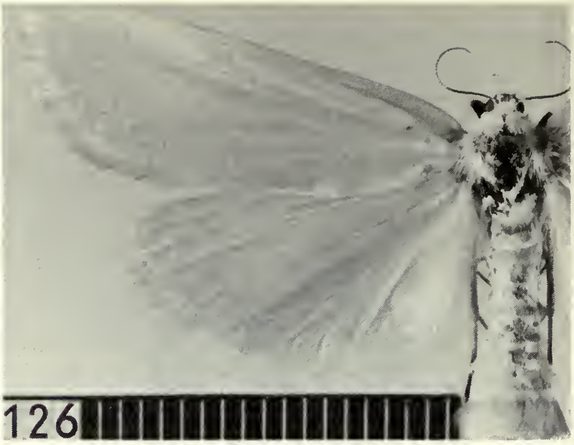


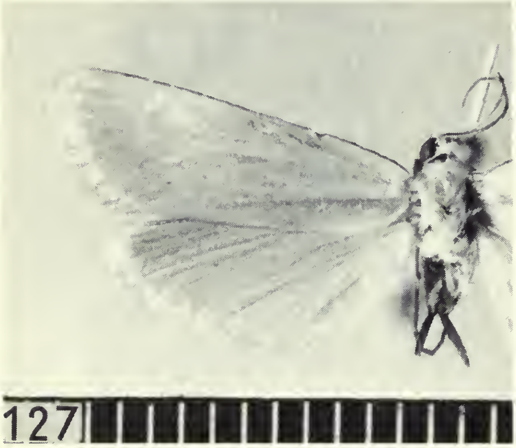
Figs 121, 122 Female genitalia. 121, *Scirpophaga incertulas* (Walker). 122, *S. innotata* (Walker).

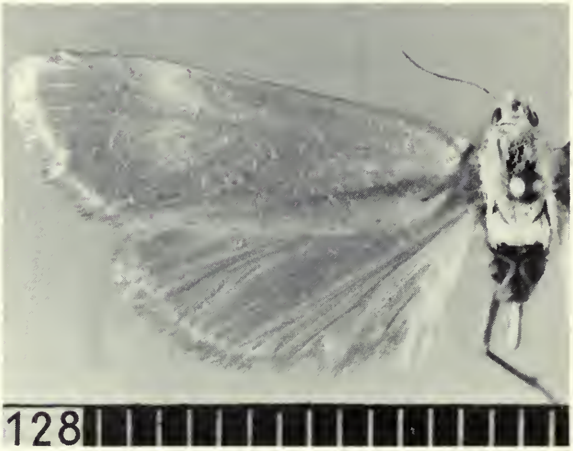


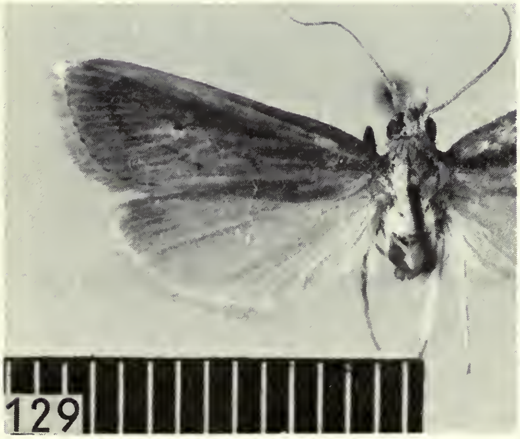
Figs 123, 124 Female genitalia. 123, *Scirpophaga lineata* (Butler). 124, *S. whalleyi* sp. n.

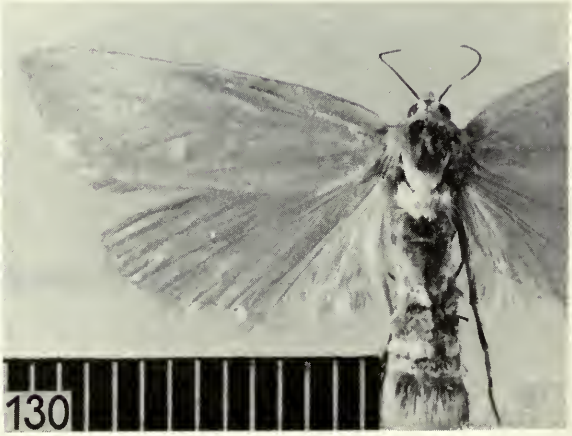




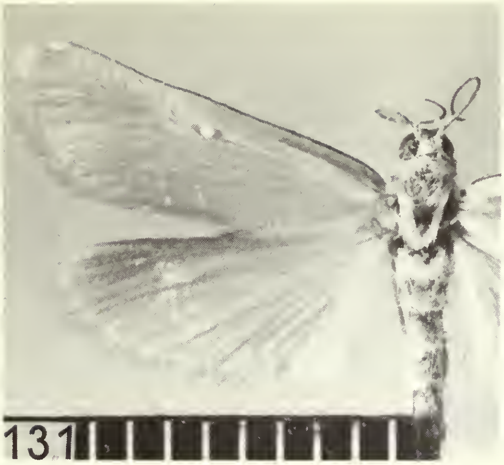


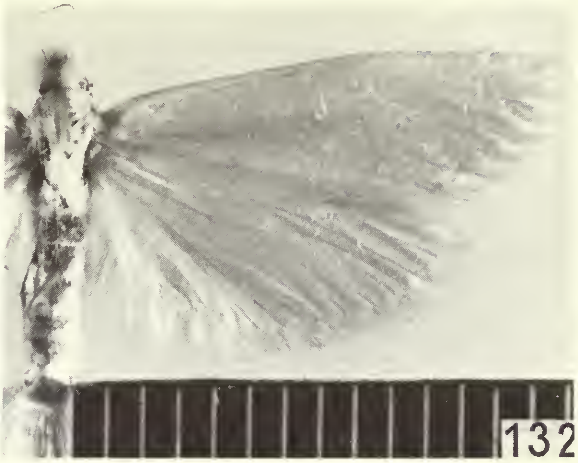


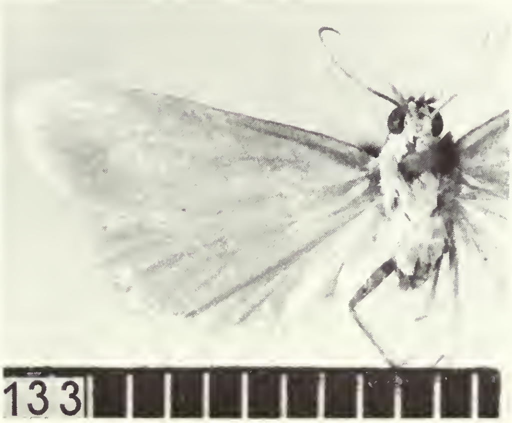


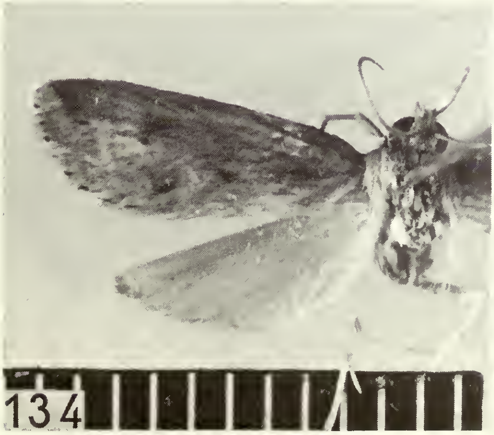


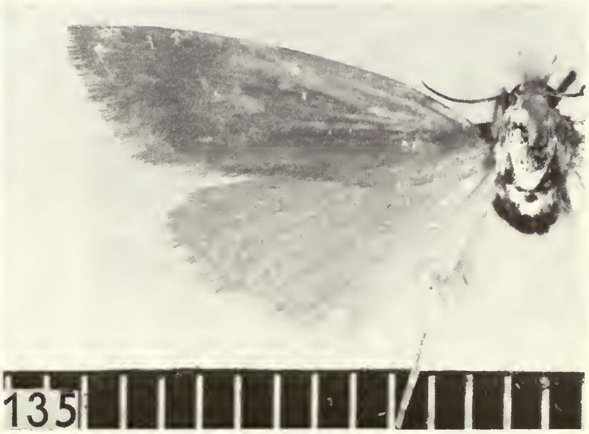
Figs 125–130 *Scirpophaga* species. 125, *S. praelata* (Scopoli), ♂; 126, *S. praelata* (Scopoli), ♀; 127, *S. xanthopygata* Schawerda, ♂; 128, *S. xanthopygata* Schawerda, ♀; 129, *S. nivella* (Fabricius), ♂; 130, *S. nivella* (Fabricius), ♀.


131

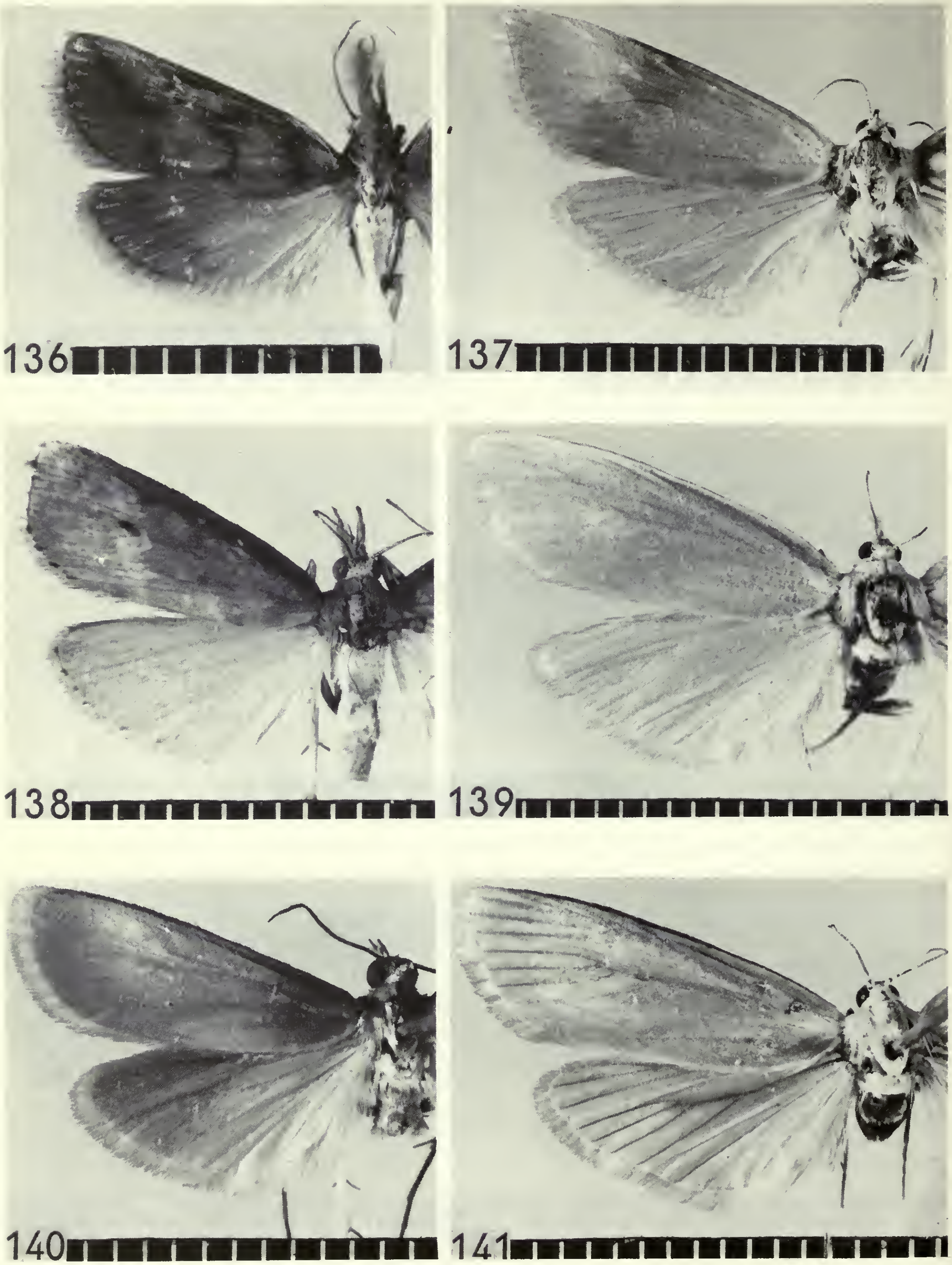

132


133

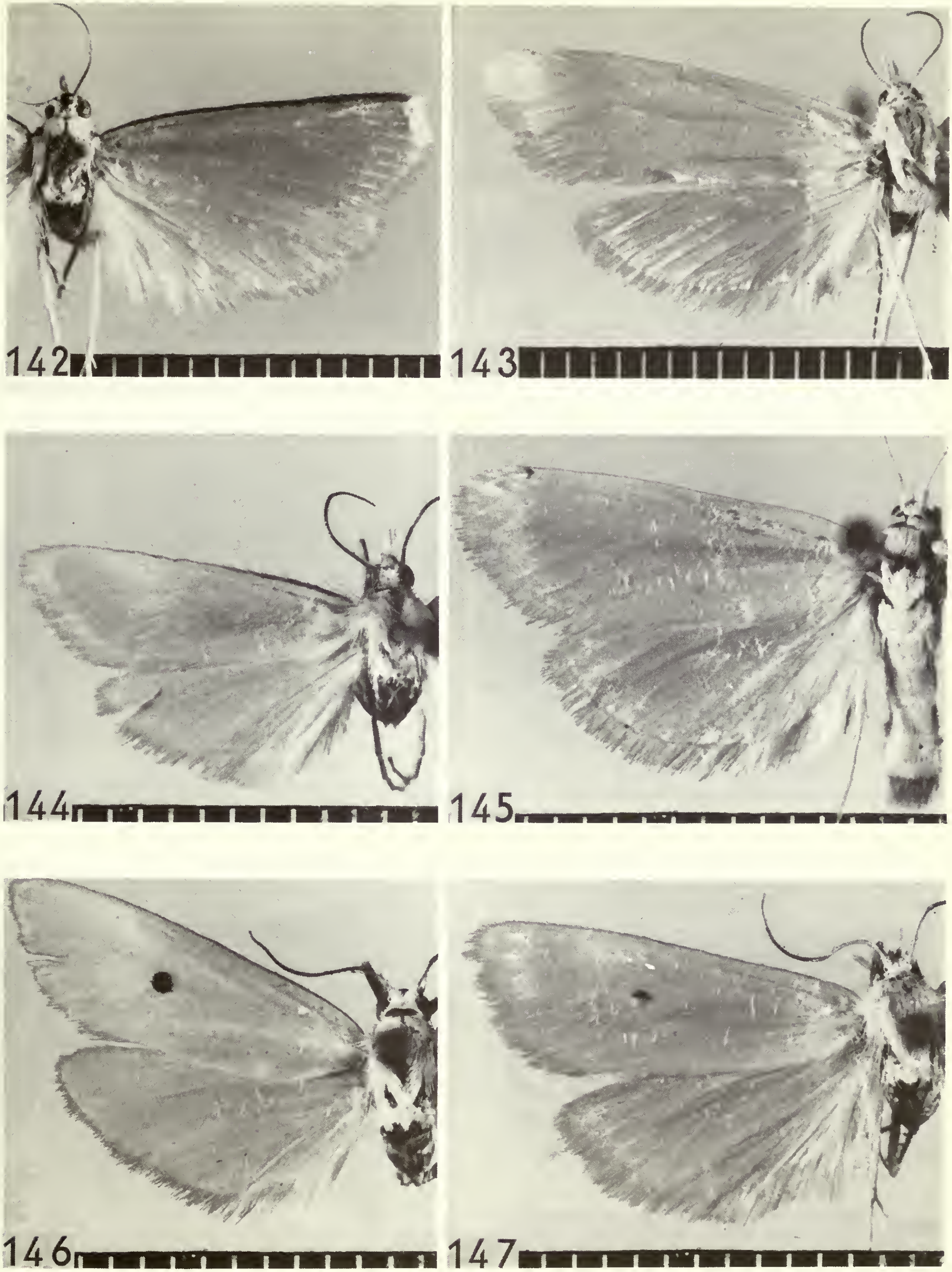

134


135

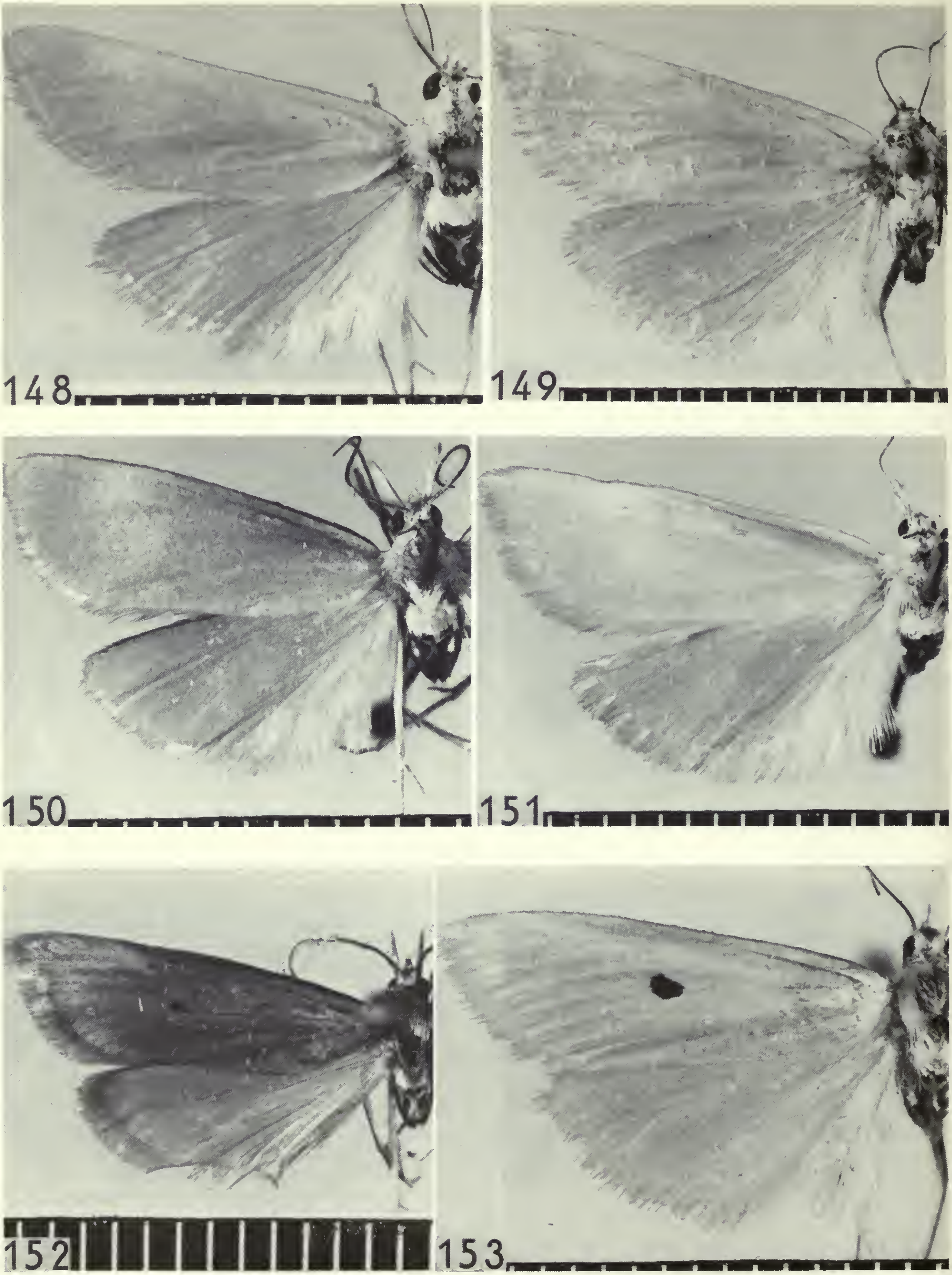
Figs 131–135 *Scirpophaga* species. 131, *S. parvalis* (Wileman), ♂; 132, *S. parvalis* (Wileman), ♀; 133, *S. phaedima* Common, ♂; 134, *S. gilviberbis* Zeller, ♂; 135, *S. gilviberbis* Zeller, ♀.


136
137
138
139
140
141

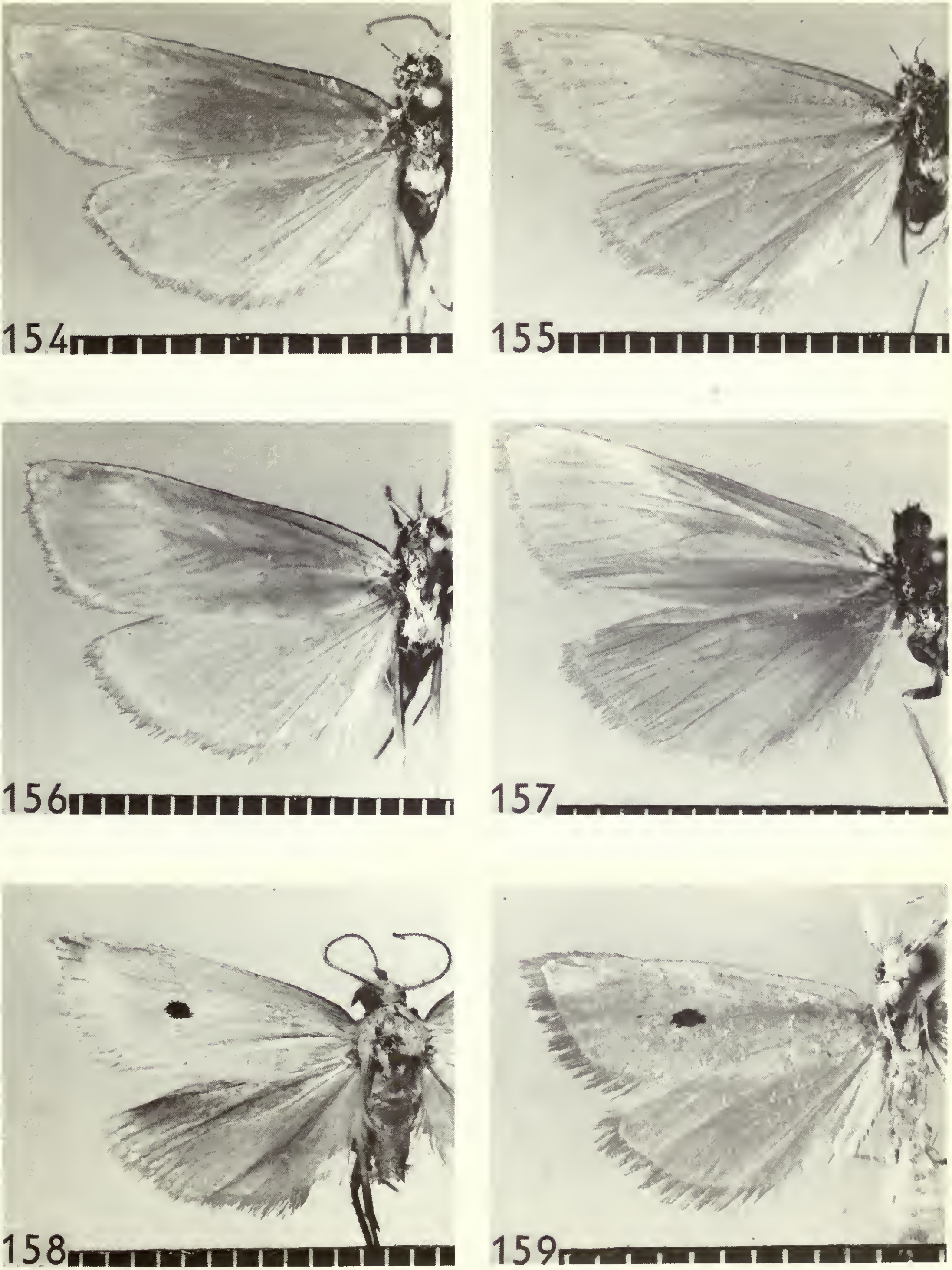
Figs 136–141 *Scirpophaga* species. 136, *S. percna* Common, ♂; 137, *S. percna* Common, ♀; 138, *S. imparella* (Meyrick), ♂; 139, *S. imparella* (Meyrick), ♀; 140, *S. xantharrenes* Common, ♂; 141, *S. xantharrenes* Common, ♀.



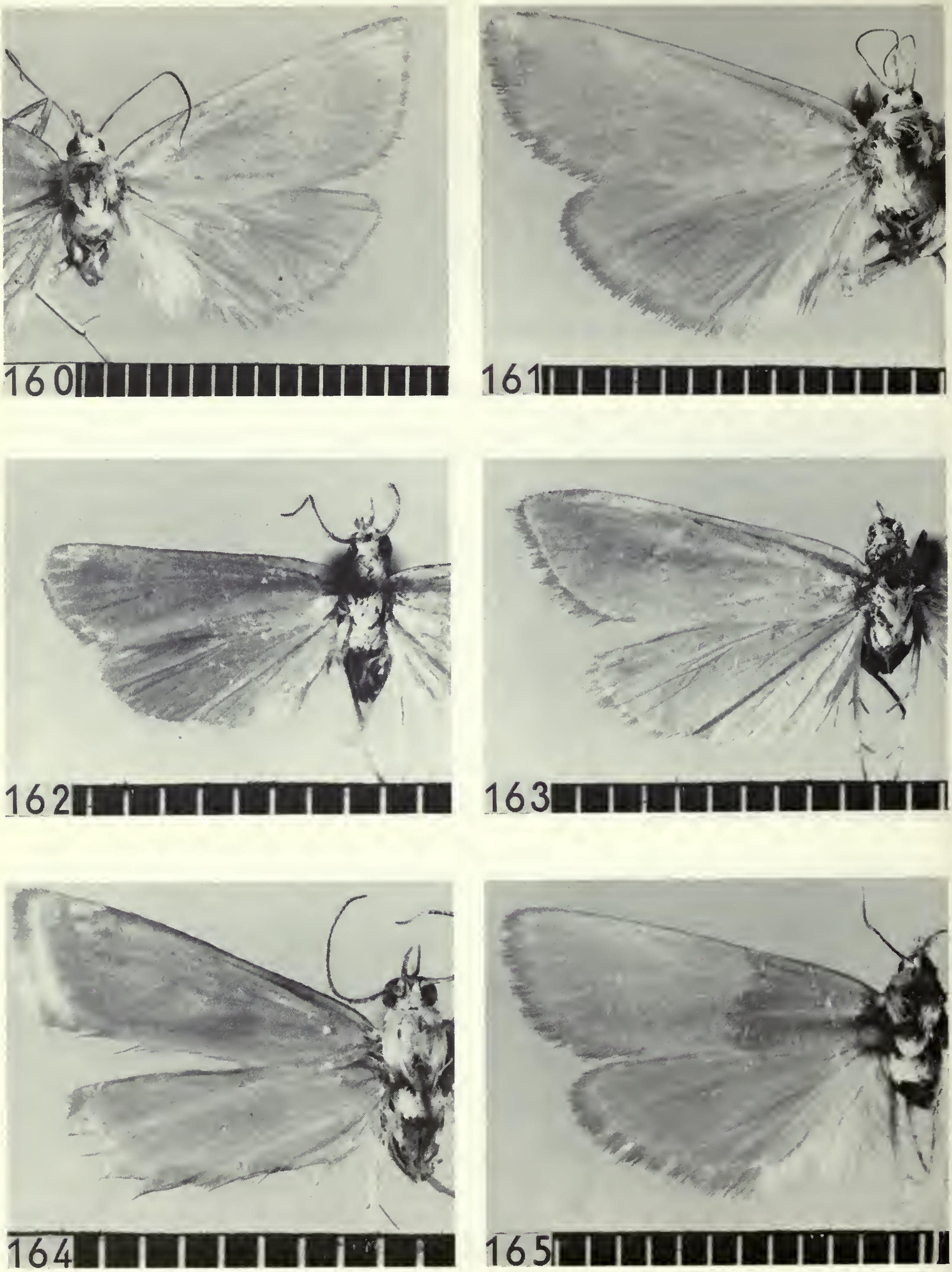
Figs 142–147 *Scirpophaga* species. 142, *S. melanoclista* Meyrick, ♂; 143, *S. melanoclista* Meyrick, ♀; 144, *S. excerptalis* (Walker), ♂; 145, *S. excerptalis* (Walker), ♀; 146, *S. excerptalis* (Walker), ♂; 147, *S. magnella* de Joannis, ♀.



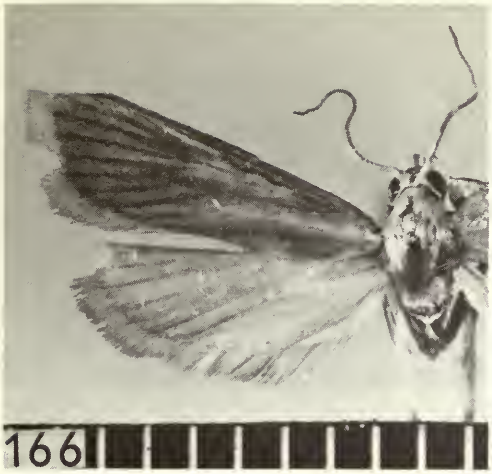
Figs 148–153 *Scirpophaga* species. 148, *S. magnella* de Joannis, ♂; 149, *S. magnella* de Joannis, ♀; 150, *S. xanthogastrella* (Walker), ♂; 151, *S. xanthogastrella* (Walker), ♀; 152, *S. brunnealis* (Hampson), ♂; 153, *S. khasis* sp. n., ♂.

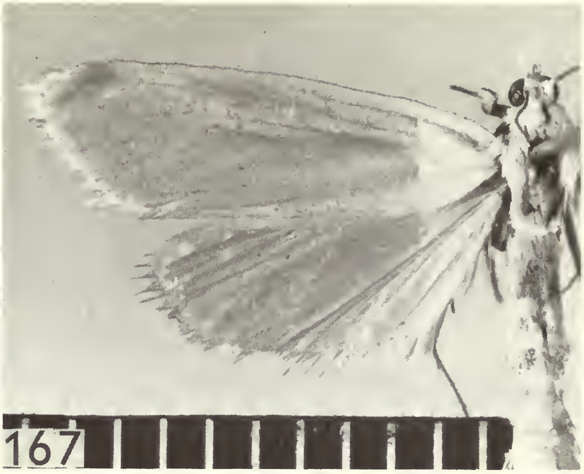


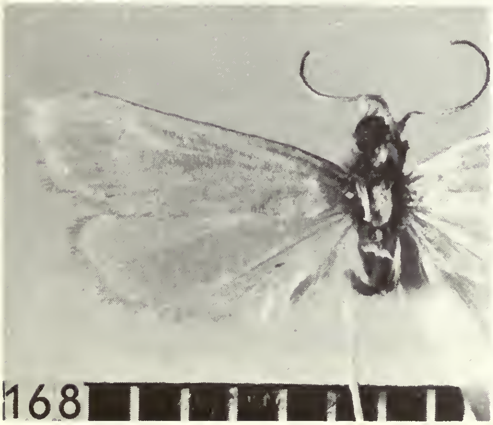
Figs 154–159 *Scirpophaga* species. 154, *S. ochritinctalis* (Hampson), ♂; 155, *S. ochritinctalis* (Hampson), ♀; 156, *S. bradleyi* sp. n., ♂; 157, *S. bradleyi* sp. n., ♀; 158, *S. flavidorsalis* (Hampson), ♂; 159, *S. melanostigma* (Turner), ♀.

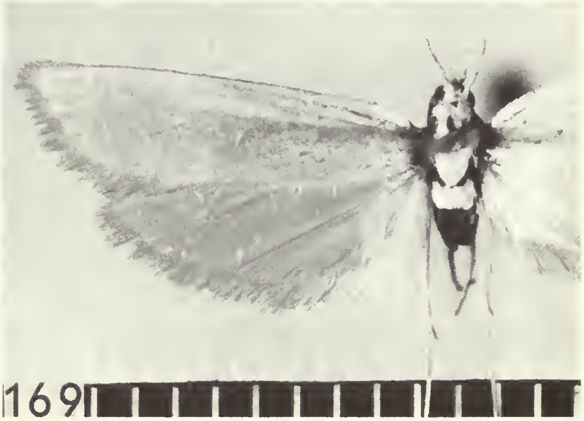

160
161
162
163
164
165

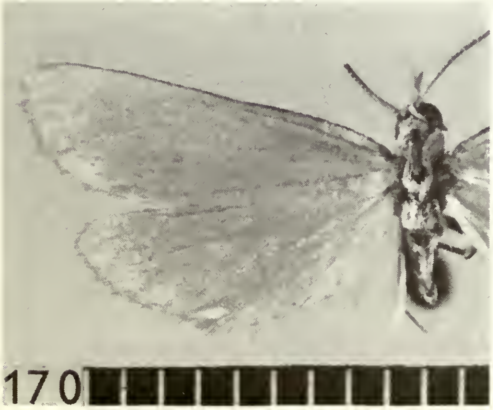
Figs 160–165 *Scirpophaga* species. 160, *S. tongyaii* sp. n., ♂; 161, *S. tongyaii* sp. n., ♀; 162, *S. occidentella* (Walker), ♂; 163, *S. occidentella* (Walker), ♀; 164, *S. fusciflua* Hampson, ♂; 165, *S. fusciflua* Hampson, ♀.

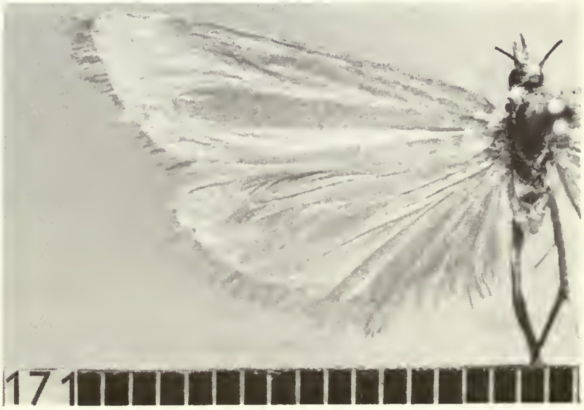

166


167

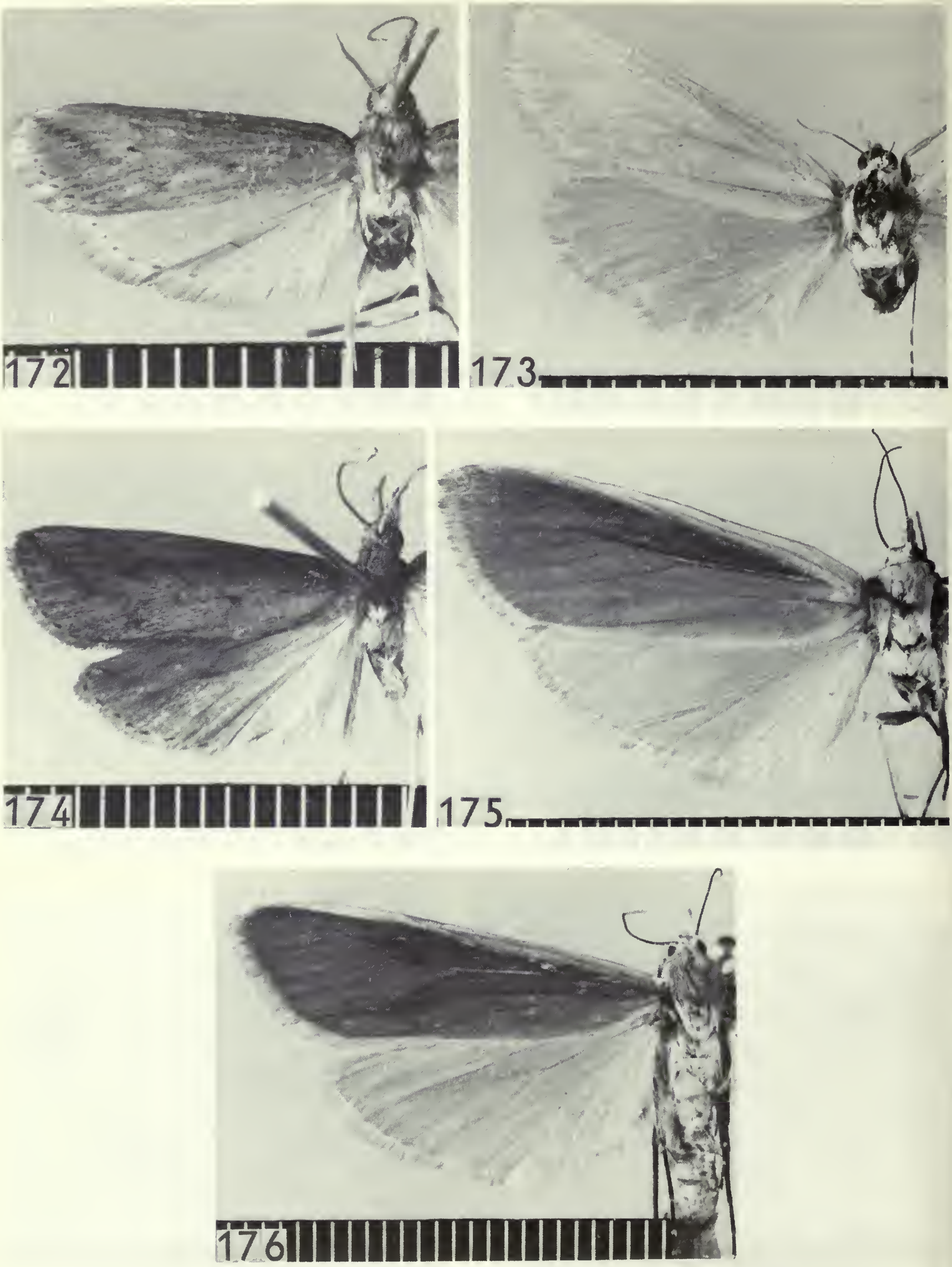

168


169

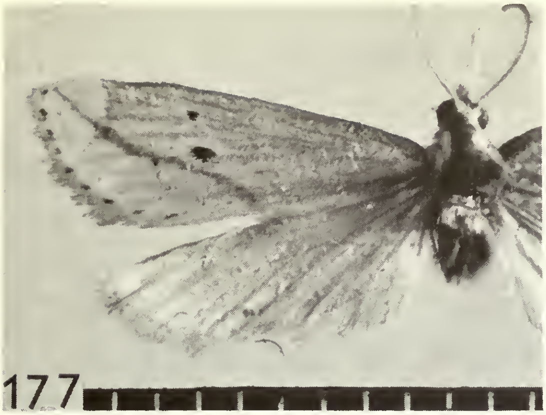

170

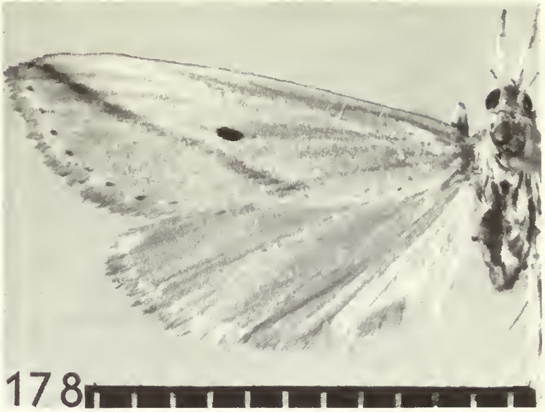

171

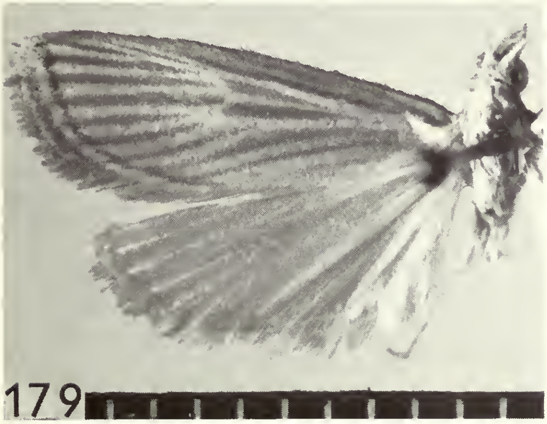
Figs 166–171 *Scirpophaga* species. 166, *S. ochroleuca* Meyrick, ♂; 167, *S. ochroleuca* Meyrick, ♀; 168, *S. virginia* Schultze, ♂; 169, *S. virginia* Schultze, ♀; 170, *S. subumbrosa* Meyrick, ♂; 171, *S. subumbrosa* Meyrick, ♀.

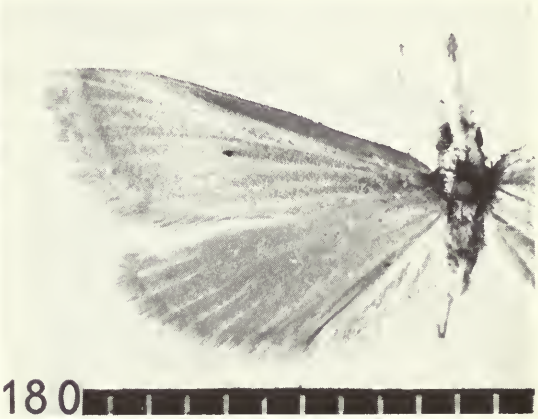


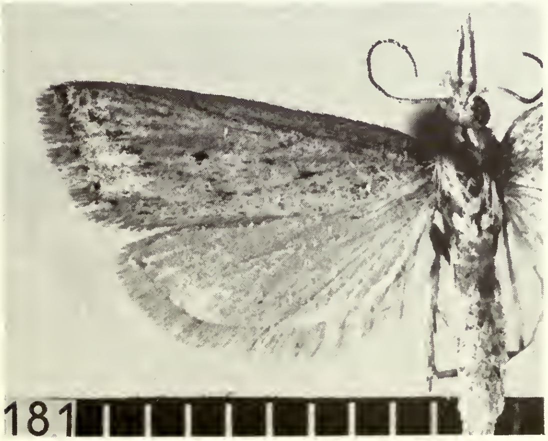
Figs 172–176 *Scirpophaga* species. 172, *S. marginepunctella* (de Joannis), ♂; 173, *S. marginepunctella* (de Joannis), ♀; 174, *S. serena* (Meyrick), ♂; 175, *S. serena* (Meyrick), ♀; 176, *S. goliath* Marion & Viette, ♀.

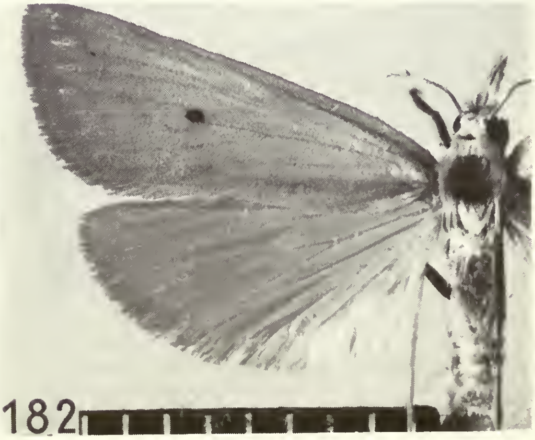




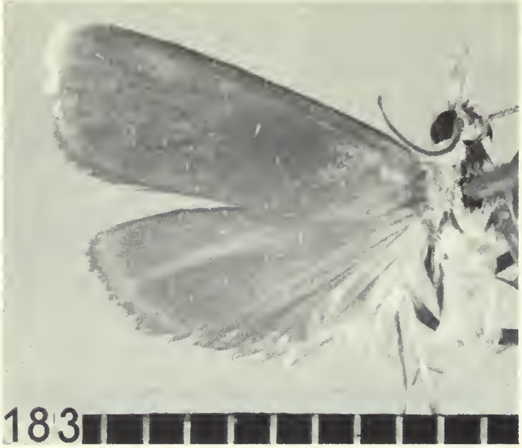


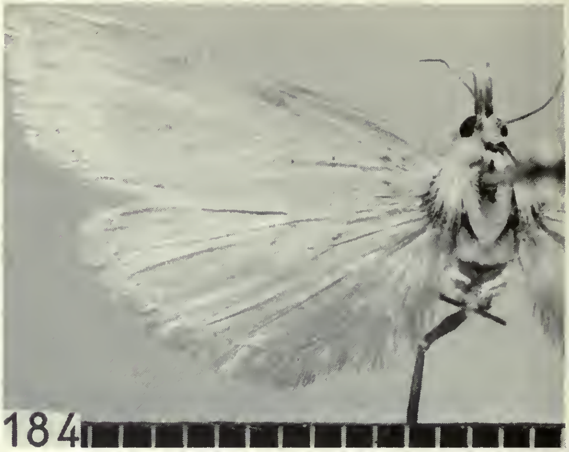


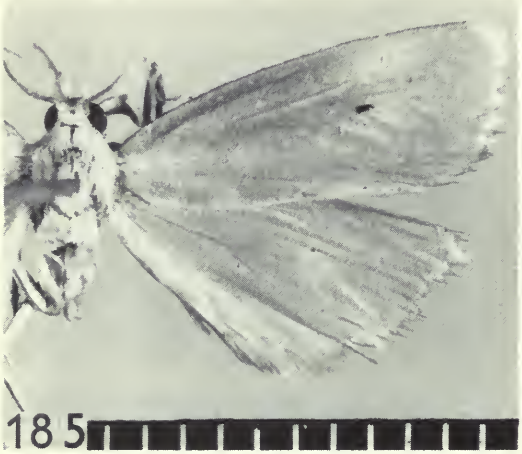


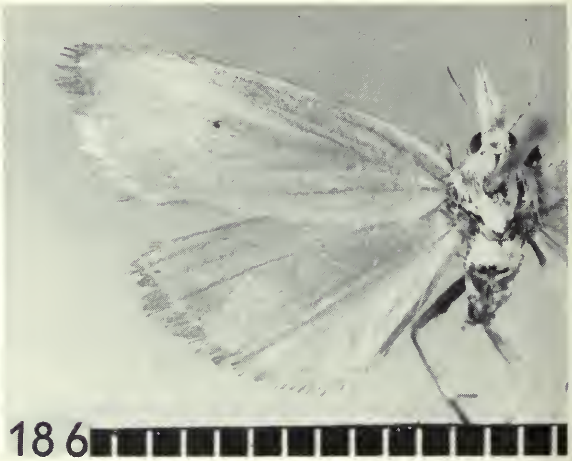


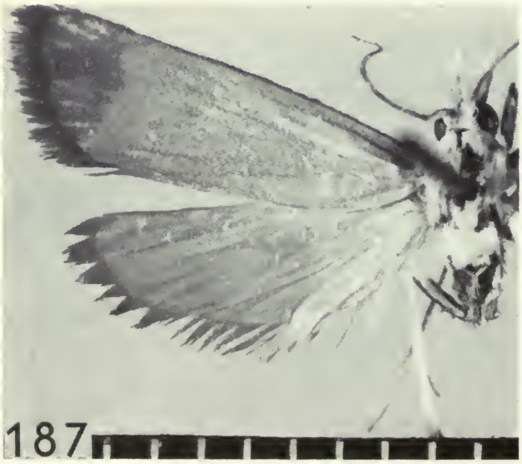
Figs 177–182 *Scirpophaga* species. 177, *S. lineata* (Butler), ♂; 178, *S. lineata* (Butler), ♀; 179, *S. aurivena* (Hampson), ♂; 180, *S. auristrigella* (Hampson), ♂; 181, *S. incertulas* (Walker), ♂; 182, *S. incertulas* (Walker), ♀.

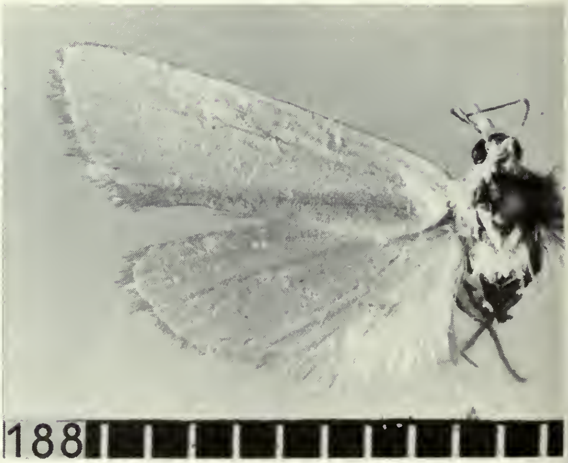












Figs 183–188 *Scirpophaga* species. 183, *S. innotata* (Walker), ♂; 184, *S. innotata* (Walker), ♀; 185, *S. gotoi* sp. n., ♂; 186, *S. gotoi* sp. n., ♀; 187, *S. whalleyi* sp. n., ♂; 188, *S. whalleyi* sp. n., ♀.

Index

Invalid names are in *italics;* principal references are in **bold.**

Acentria 188
Adelpherupa 189
admotella 190, **243**
alba 190, **205,** 206
albinella 190
Apurima 187, **190,** 196
Argyractini 188
Argyrostola 189
auriflua 190, **211**
auristrigella 193, 240, 241, **242**
aurivena 193, 240, 241, **242**

bipunctifera 190, **243**
bradleyi 192, 202, 222, 223, **229,** 230, 232
brunnealis 192, 217, 222, **228**
brunnescens 191, **211,** 212
butyrota 211, 214, **223,** 224, 226

Calamoschoena 188
cargaritifera 188
Catagela 189, 191, 196
celidias **211,** 214
Chilo 190
chionotus 217
chrysorrhoa 190, 191, **211,** 212
cinerea 190, **205,** 206
costalis 227
Crambinae 189–191
Crambostenia 189

Donacaula 189, 190, 196
dubia 190, **205**

elachia 217
Erupa 189
euclastalis 211
excerptalis 185, 190–192, 194, 198, 201, 209, 212, 213, 222, **223,** 224–228, 230
excerptalis-group 185, 193, 201–203, 209, **222**

flavidorsalis 192, 194, 222, **230,** 231
flavus 189
fusciflua 192, 233, **234,** 235–237

Gabalaeca 189
gilviberbis 190, 192, 194, 195, 203, 204, **216,** 217, 218, 234
gilviberbis-section 203, 204
goliath 193, 233, 234, **239,** 240
gotoi 193, 203, **249**
gotoi-group 185, 203, **249**
gratiosellus **243,** 244, 246
grisea 205, 206

hoplites 217
helodes 191, **219,** 220
Helonastes 187, 189, 191, 196

incertulas 190–195, 212, 218, **243,** 244, 247, 249, 251
incertulas-group 185, 201, 203, **242**
innotata 190–196, 243, 244, **246,** 247
intacta 223
intactella 189
imparella 191, 192, 195, 203, 204, 218, **219,** 220

khasis 192, 222, **230**

Lancia 189
latidactyla 190, **205**
Leechia 188, 189
leucatea 190
lineata 193, 194, **240,** 241, 242
lineata-group 185, 201, 203, **240**
limnochares 191, **205,** 206, 209

macrostoma 229
magnella 192, 222–224, **226,** 228, 230
marginepunctella 192, 233, 237, **238,** 239
melanoclista 192, 203, 204, **221**
melanostigma 192, 194, 222, 223, 226, **231,** 232
melitopsis 189
minutellus 190, **243,** 244, 246
monostigma 190, **223,** 224, 228

Neerupa 189
Neoschoenobia 188, 189
nigropunctata 189
Niphadoses 187, 191, 196, 217
Niphopyralis 188, 189
nivella 191, 192, 194, 195, 203, 204, 209, **211,** 213, 216, 218, 222–224, 227, 238, 244
niveus 211
Nymphulinae 188

occidentella 190, 192, 233, **234**
occidentella-group 185, 193, 201, 203, **233,** 237, 239, 249
ochritinctalis 192, 222, 223, **229,** 230, 232
ochroleuca 191, 192, 194, 233, 234, **235**

palleucus 217
pallidalis 188
parvalis 192, 193, 203, 204, **214,** 215
Patissa 189
percna 191, 192, 194, 195, 203, 204, **218,** 221
percnopsis 189
phaedima 191, 192, 195, 203, 204, **215,** 216
phantasmatalis 205
phantasmatella 189, 190, 195, **205,** 206
phantasmella 189, 190, 195, **205,** 206
praelata 185, 190–204, **205,** 206, 209, 211
praelata-group 185, 193, 201, **203,** 204, 218, 221, 240, 249

praelata-section **203,** 204, 217
Promacrochilo 189
punctellus 190, **243**
pyraustalis 188
Pyraustinae 188

quadripunctellifera 243

Ramila 188, 189
rhodoproctalis 223
Rupela 188, 190, 191, 193

Schoenerupa 189
Schoenobiinae 185, **188,** 189–191, 196, 201
Schoenobius 187, 189–191, 196
Scirpophaga 185–187, 189–194, **195,** 196, 201, 202, 206, 243
serena 192, 233, 234, 238, **239**
sericea Passerini 190
sericea Snellen 247
Siga 191
Siginae 191
subumbrosa 192, 233, **237,** 238

Tephroniopsis 189
Thopeutis 190
Tipanaea 188, 190, 191
tongyaii 192, 222, 223, **232**
Topeutis 187, 190, 191
Tryporyza 191, **196,** 243

virginea 189, 190
virginia 185, 192, 233–235, **236**, 237

whalleyi 193, 194, 202, 203, **251**
whalleyi-group 185, 202, 203, **250**

xantharrenes 191, 192, 195, 203, 204, 218, **221**
xanthogastrella 190, 192, 194, 196, 222, 223, **227,** 228
xanthoperas 189
xanthopygata 185, 192–194, 203, 204, 206, **209,** 211, 215

Zolea 189

British Museum (Natural History) Publications

Catalogue of the Diptera of the Afrotropical Region

Editor: R. W. Crosskey. *Assistant editors:* B. H. Cogan,
P. Freeman, A. C. Pont, K. G. V. Smith and the late H. Oldroyd.
British Museum (Natural History). 1980, 1437 pp. £55·00

The Diptera or two-winged flies are probably the most important insects that affect man. Although most flies are harmless, some have become transmitters of dangerous diseases to man and his domestic animals, and others are important pests of agricultural crops. Some flies are beneficial because they destroy large numbers of plant-feeding insects through their parasitic or predacious habits.

Nowhere is their socio-economic and medical impact more sharply felt than in tropical Africa, where fly-borne diseases are not only a direct health hazard but can prevent or hinder development of the land. The control of such diseases as sleeping sickness and onchocerciasis depends in great measure upon controlling the flies that carry them. This in turn requires a thorough appreciation of all that is known about the insect vectors, including their basic taxonomy, so that they can be correctly identified and their geographical ranges accurately established.

This catalogue synthesizes the scattered basic taxonomic work on the Diptera of tropical Africa and its islands by listing the known 16,500 species with their synonyms and known geographical ranges within a comprehensive classification. A short introduction is given to each family and a bibliography of 4,700 titles provides references to the primary literature. Such a task has never before been attempted for the region and its completion should greatly stimulate taxonomic research. The *Catalogue* represents ten years' careful work by a team of forty specialists, under the editorship of six dipterists on the staff of the Natural History Museum, themselves contributors with considerable expertise in the African fauna.

The *Catalogue* should serve for a long time as an indispensable tool to the taxonomist and an essential source-work to anyone concerned with African flies in the fields of medical, agricultural and veterinary science.

Titles to be published in Volume 42

A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. By Michael C. Day.

A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. By Barry Bolton.

A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). By J. Mark Ritchie.

A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). By Angoon Lewvanich.

Printed by The Whitefriars Press Ltd, London and Tonbridge